

STUDIES in the POST-SEMINAL DEVELOPMENT of the

MONOCOTYLEDONOUS EMBRYO

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REGISTER OF PLANTS

1.

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INTRODUCTION

Before considering the aims and scope of the present research, previous work on the initial stages in the life history of Monocotyledons, and the lines of investigation suggested by them, will be briefly considered.

HISTORY OF RESEARCH ON THE MONOCOTYLEDONOUS EMBRYO AND SEEDLING

As SARGANT (106) has suggested there were three phases in the history of the research. The school of purely external morphology represented by IRMISCH was succeeded by the students of early embryology, whose work was made possible by the invention of the compound microscope. HANSTEIN'S researches having for their aim the discovery of an apical meristematic cell in seedlings not only contributed a great deal to the knowledge of embryos but acted as an impetus to investigators who followed. Later workers concentrated on the post-seminal stages in the plant's development. Modern improvements in microscopy and in the technique of sectioning and staining made it possible not only to supplement earlier work, but also/

also with seedling anatomy as the basis, to formulate theories of phylogenetic significance. The extent of the literature published since the beginning of the present century is an indication of the interest aroused in this type of investigation, in which comparative morphology and anatomy are frequently used as tools in fashioning a theory and not ends in themselves.

SCOPE OF THE LITERATURE, BRIEFLY CONSIDERED

As reference to the bibliography (Vol. II) will show, a considerable bulk of literature on the seedling and embryo exists but much of it is somewhat limited in scope.

- i. Many publications are devoted to families in which the seed is easily obtainable or in which germination takes place readily, e.g. Liliaceae, whereas families such as Bromeliaceae and Marantaceae are practically untouched.
- ii. Little or no account is to be found of the early stages in the lives of the commonest British plants.
- iii. Even in cases where information on the germination and external morphology of the seedling is/

is available, anatomical details are often lacking. This criticism naturally applies most to the early literature. It is to be regretted that it is also true of a few recent papers.

iv. Modern research is increasingly directed to the cytology of the embryo. Accordingly it is commonly found that accounts of the embryo are concerned principally with proembryonic stages concluding with a brief reference to the ripe embryo.

v. Lastly except for two isolated publications by GATIN summarising the results of research on seedlings of Palmae, Cannaceae and Musaceae, no attempt, as far as is known, has been made since the time of KLEBS and SCHLICKUM to collect and co-ordinate the literature on seedlings even for single families or cohorts.

Many of these discrepancies are made evident by a consideration of the chapter on the seedling and its significance in the most recent Monograph on Monocotyledons (3).

ARRANGEMENT OF THE LITERATURE
IN THE FOLLOWING RESUME

The literature will be arranged not in chronological order but according to the aspect of the seedling of which it treats. But as comparative anatomy, with phylogenetic aims was preceded by embryology and, earlier still, by external morphology the separation in this discussion into morphological, anatomical and phylogenetic problems is in a certain measure corresponding to a separation in time.

A. MORPHOLOGY OF THE SEEDLING

I. EXTERNAL MORPHOLOGY OF GERMINATION.

KLEBS, in the introduction to his well known publication of 1871, gave an account of his predecessors in research on seedlings - DE CANDOLLE, RICHARD MIRBEL, the pure morphologists; WARMING, CASPARY, WINKLER and SACHS whose interest was centred on the physiological aspect; but as he pointed out, up to that time the biological significance of the different forms of germination had been totally neglected. A study of the seedling ought to take into account factors such as conditions of life of the adult, time, duration and course/

course of germination, geographical distribution and the natural affinities of the different genera. A composite picture of germination was required into which both morphology and physiology would enter, which would show how the young plant responded to the environmental conditions and which would explain many diversities left obscure by a purely physiological interpretation.

Having examined numerous seedlings and searched the literature for further information, KLEBS proceeded to classify germination under seven headings -

- Type I. Primary root emerges first and exhibits strong growth. One end of the cotyledon remains in the seed, the other forms a short sheath.
- Type II. As in I. but the cotyledon sheath lengthens considerably and a filiform stalk connects seed and sheath.
- Type III. Germination of the Gramineae.
- Type IV. Cotyledon sheath first produced. Radicle grows in length later. This is the Cyperus - Carex type.
- Type V. Primary Root grows actively. The cotyledon becomes aerial and is the first foliage leaf.
- Type VI. A ring of root hairs is produced at the upper limit of the root which at first is undeveloped. Cotyledon as in V. - typical for aquatics.
- Type VII Germination of the Orchidaceae.

A critical survey of this classification will be made in the final discussion. It will suffice to note here that KLEBS, whether intentionally or not, makes no distinction between ligulate and non-ligulate cotyledons, and includes ligulate types in both Types II. and V.

2. EXTERNAL MORPHOLOGY OF THE COTYLEDON.

KLEBS noted that for related forms the type of germination and therefore shape of the cotyledon was variable and that the duration of the latter organ might be restricted to a few weeks or extend to two years. No explanation of these features was offered. It remained for SCHLICKUM, in 1896, to co-ordinate the variations in form shown by the cotyledon and to try to discover whether the epigeal cotyledon gave rise to the complex Grass type or vice versa. This merits a more complete discussion which will be given later. SCHLICKUM'S is the first and still one of the very few attempts to account for the ligulate type of cotyledon.

LUBBOCK, in 1892, had included types of monocotyledonous germinations in his purely descriptive work on seedlings.

3. PROBLEMS ARISING OUT OF THE EXTERNAL MORPHOLOGY.

1. Morphological significance of the single cotyledon; its suggested origin.

- (a) JUSSIEU believed that the cotyledon was equivalent to the first foliage leaf of the plant which had taken on special functions, e.g. the absorption of endosperm. The terminal position of the organ raised difficulties in accepting this interpretation of it.
- (b) LYON () bearing in mind its haustorial function believed that the cotyledon was equivalent to the "foot" of the Vascular Cryptogams.
- (c) BALFOUR (7) rejected the idea that it was either a leaf or the homologue of the lateral cotyledons in the Dicotyledons.
- (d) SARGANT is the chief exponent of the theory that the cotyledon is the equivalent of the two cotyledons of the Dicotyledons which have fused. This conclusion was formed as the result of a study of Liliaceous seedlings. A comparison of the seedling of *Anemarrhena* with Ranalean forms provided the main evidence for the theory. As to the position of the/
the/

the single cotyledon, she maintains that "if it be derived from the two cotyledons of an ancestor, it cannot really be terminal" (102). Certain advantages she declares, accrue to the plant in virtue of its adoption of monocotyly. Shortening and thickening of the hypocotyl, the formation of perennating organs, and economy of material for seed leaf tissue are the results of Syncotyly.

- (e) COMPTON (28) upholds the theory of Syncotyly but differentiates between symmetrical fusion along both edges in albuminous seeds or fusion along one edge in exalbuminous seeds such as the Helobieae.
- (f) HILL (60) from a study of geophilous species of *Peperomia* in which a division of labour in the seedling occurs, one cotyledon being set free, the other acting as a sucker in the seed, opposes SARGANT'S view. He thinks that "the monocotyledonous habit is due to the adaptation of the two cotyledons to specialised functions". The first foliage leaf is comparable to the second cotyledon.

(g)/

- (g) HENSLOW considers that the suppression of one of the two cotyledons is only another indication that the monocotyledons are degenerate, as a result of self adaptation to a moist or aquatic habit.
- (h) From a research on the embryo and seedling of a species of *Agapanthus* (Amaryllidaceae), which could have one or two cotyledons, COULTER and LAND decided "that cotyledons are always lateral structures arising from a periphery zone at the top of a more or less massive proembryo. This reduces cotyledony in general to a common basis in origin, the number of cotyledons being a secondary feature". Monocotily is not due to the union of two cotyledons or the suppression of one, but is the continuation of one growing point on the zone producing cotyledons.
- (i) WORSDELL (129) states it as his opinion that the cotyledon is homologous with the seta of Bryophyta (cf. LYON).
- (j) ARBUR (3) deplores the tendency to treat cotyledons as organs apart and would prefer the/

the standpoint "that one section of the Flowering Plants is monocotylar - not because there has been a fusion of two leaves, nor because there has been suppression or displacement of the second - but because the growth-rhythm happens to be of the type which produces a single leaf at the first node". The occurrence of sheathing leaf bases "absolutely precludes the production of two leaves at a node".

ii. Relation of the Cotyledon to the First Leaf.

- (a) It was observed by KLEBS that, while in many families the shape of the cotyledon was sharply demarcated from that of the first leaf, in others the two resembled each other. In plants which produced first leaves simpler than the adult leaf it was possible to follow a transition from the cotyledon to the first true foliage leaf. In such cases it was justifiable to trace the primitive type back to the cotyledon.
- (b) SCHLICKUM'S research dealt almost entirely with the comparative anatomy of first leaf and cotyledon. There was a striking resemblance in the structure of both organs in aquatic plants/

plants, a similarity which was lacking where the cotyledon was hypogeal and ligulate.

- (c) From a consideration of the symmetry of both organs SARGANT thought it most improbable that the first leaf is a transformed cotyledon. HILL'S theory regarding the origin of monocotyledons has been mentioned; he looks upon the first leaf of an abnormal *Arisarum* (60) as showing by its behaviour a lost function and indicating the possibility of its being a second cotyledon.
- (d) COMPTON noted (28) that the cotyledon anatomy may be shared by the succeeding leaf if it draws its vascular supply direct from the root.
- (e) AREER states that in anatomy as well as phyllotaxis the early leaves (i.e. cotyledon and first plumular leaf) hark back to the structure of the root with which they are in continuity.

4. RELATION BETWEEN THE FORM OF THE EMBRYO AND THE TYPE OF GERMINATION.

The only investigator who treats of this is GATIN/

GATIN who discovered that in Palmae, Cannaceae and Musaceae, a definite connection exists. His findings will be later discussed.

B. PROBLEMS CONNECTED WITH THE VASCULAR ANATOMY.

The most striking use of the vascular skeleton as the basis of a theory is afforded by SARGANT'S work. Her theory of the origin of monocotyledons was indeed founded on the seedling structure of the Liliaceae. Great stress was laid on the transition phenomena as a guide to relationships within the family. SARGANT was able to add a fourth, the Anemarrhena Type, to VAN TIEGHEM'S three types of transition. The various theories of the nature of the transition, all founded on the examination of seedlings have been summarised and criticised by COMPTON (27).

By botanists such as VAN TIEGHEM, GRAVIS and CHAUVEAUD who sought to elucidate the true relation of primary root to primary stem, attention was focussed on the hypocotylar structure. Their aim was not to add to the stock of knowledge on seedlings, for they divorced its vascular anatomy from its phylogeny/

phylogeny, general morphology and habit. The same remark applies also to the work of JEFFREY (77) on the central cylinder of Angiosperms with a view to finding what was the primitive condition of the stele. He decided that it was tubular interrupted by foliar lacunae corresponding to the leaf traces; formation of intrastelar pith is also discussed in his paper. CHRYSLER'S (26) later research on similar lines was confined to the families Araceae and Liliaceae.

C. THE SEEDLING AND ITS PHYLOGENETIC SIGNIFICANCE.

That the seedling has a phylogenetic significance at all has been the subject of much controversy as the following account will reveal. Almost all recent research on seedlings, monocotyledonous and otherwise, has been directed to this aspect.

The term "phylogeny" has been used by different authors to suggest varying degrees of relationship. In its widest sense, it connoted the relationship between the two great groups of Angiosperms, and is used frequently in this connection. It may also be applied to the affinity of one family to another or of genus to genus in the same family and in this more limited/

limited interpretation occurs less often, since seedling anatomy aroused interest principally as a clue to the origin of Monocotyledons and Dicotyledons and not as an aid to the systematist.

1. Opinions that the seedling structure indicates phylogeny.

1. As already noted, SARGANT raised the question in discussing the significance of the seed leaf as a basis for classification. She proceeded to show from an investigation of the anatomy of sixty genera of the Liliaceae (103) that an argument for the derivation of the Monocotyledon from a dicotylous stock could be built up on anatomical evidence.

The possibility of the seedling as an organism revealing generic links within the Liliaceae was, however, not lost sight of and the anatomy of transition used as a basis for this. Several years after the publication of the results of this research, which aroused a certain amount of criticism, SARGANT still held the opinion that the comparative anatomy of the seedling had a place in the solving of phylogenetic problems as is shown by her statement/

statement in 1914 - "There is no glaring improbability in the suggestion that the vascular system of the young seedling may afford a clue to the structure of a remote ancestor" and again, "The connection between embryology and systematic botany must be close but the exact nature of the connection is yet undetermined.....Conclusions from the new embryology sometimes appear to conflict with the results of systematic botany. It does not necessarily follow that embryological evidence is of no systematic value".

- ii. SARGANT'S claim that the hypocotyl is the structure least affected by external factors is supported to a certain extent by the work of TANSLEY and THOMAS which extended the survey to Cycads and Dicotyledons. They found both simple and complex types in the hypocotyl but the same type occurred in allied species of totally different habit.
- iii. Referring to the embryo, GATIN, in 1906, remarks "L'étude approfondie de l'embryologie et de l'embryogénie des groupes peut seule apporter quelque lumière sur les relations phylogéniques/

phylogéniques qui les retient entre eux".

2. Opinions that seedling structure does not indicate phylogeny.

- i. A. W. HILL (60) from a study of species of *Peperomia* opposed SARGANT'S views. He doubted the value of anatomy as a key to the origin of Monocotyledons since external changes in the habitat would be accompanied by some internally, the peculiarities of the latter being the outcome of recent adaptations rather than the expression of developmental history. But SARGANT herself (105) recognised the difficulties in such work in distinguishing between "adaptive characters of comparatively recent origin and the characters inherited from remote ancestors".
- ii. GATIN (51) criticised SARGANT'S theory on the grounds that the vascular anatomy of the embryo varied according to its age. Yet SARGANT'S research dealt with seedlings, not embryos. "The skeleton may be constant for a genus or another group after (though not before) /

before) germination". (SARGANT 1908).

iii. DE FRAINE found in the seedling structure of certain Cactaceae a certain parallel between morphology and anatomy, so that seedlings could be divided into two groups, true for both features, but the structure of the vascular skeleton was useless in delimiting the genera within the groups, so she concluded that "it is impossible to define a genus in terms of its seedling structure" (44).

iv. From a survey of the structure of Proteaceous seedlings HILL and DE FRAINE, in 1912, were led to believe that anatomical detail had been so profoundly modified by morphological and physiological factors that in many cases the anatomy was useless to determine the phylogeny. In the following year they published a summary of certain facts regarding the structure of seedlings.

The following anomalies were recorded.

- (a) The Anemarrhena type is found in such widely differing groups as Ranunculaceae, Bignoniaceae and Cactaceae.
- (b) There is a resemblance between seedlings of Ranunculaceae, Piperaceae and Araceae.
- (c) Details are not constant in a single species.

(d)/

- (d) Orders and even genera which are accepted as allied show different methods of transition.

They conclude that seedling anatomy by itself is no criterion. In questionable cases it would be useless as an aid to classification.

- v. WINIFRED SMITH (117) found that in Sapotaceous seedlings the type of anatomy characteristic for the order was liable to adaptive variations.
- vi. LEE(83) who examined seedlings of Compositae is quite emphatic in the statement that there is absolutely no phylogenetic value in seedling anatomy. This opinion was based on an extensive series of observations of fifty species. It was found that variations in vascular structure occur not only in related species but in different examples of the same species.
- vii. COMPTON made a thorough research on the seedlings of Leguminosae concluding "that to a limited extent characters of seedlings may be of diagnostic value but it is exceedingly risky to apply them to solve the broader problems/

problems of phylogeny". Elsewhere he is not so non-committal in the statement of his opinion - "The search for phylogenetic relationships through the medium of seedling anatomy is a forlorn hope".

D. THE ONTOGENY OF THE SEEDLING
AS INDICATING PHYLOGENY.

That the seedling in its development recapitulated the history of the race in a manner similar to that of the Fern, according to BOWER'S Theory, was a question for speculation.

- i. SARGANT believed that the seedling "while it consists of cotyledons, hypocotyl and primary root only", (the plumule being present as a mere bud) must represent a past period in race history when its ancestor possessed an exarch stele in stem and root alike. "The cotyledon node on which the epicotyl is inserted would then mark the interval between two acts in the drama of evolution".
- ii. TANSLEY and THOMAS consider the early ontogeny to be dependent on the habit of the intra-seminal embryo and therefore untrustworthy but/

but SARGANT believes that the ancestral features would show in the early post-seminal history when they would tend to be preserved better.

- iii. HORWOOD adversely criticises SARGANT'S evidence since, in his opinion, it was based on embryological features at a stage too early for recapitulation to be observed.
- iv. CHAUVEAUD'S Theory of the Nature of the Transition and the relation of root to stem was based on an assumption that the different structures succeed one another in time. A theoretical phylogenetic sequence is realised in the ontogeny (27).
- v. COMPTON held the opinion (1912) that the prospect that the ontogeny in vascular structure would prove to repeat the phylogeny was "highly improbable".

E. FACTORS INFLUENCING THE STRUCTURE OF THE SEEDLING

The doubt that the anatomy of the seedling would indicate/

indicate the phylogeny rose from a consideration of the different influences to which it was subject.

It will be instructive to make a list from the evidence collected by different authors; several of whom have been mentioned in the preceding pages, of factors upsetting the balance of the morphological and vascular structure in the embryo and seedling. Such would tend to hide the primitive type having a simple, easily followed ontogeny which would furnish phylogenetic clues.

1. CONDITIONS AFFECTING THE FORM OF THE EMBRYO WITHIN THE EMBRYO SAC.

(a) The space at the disposal of the embryo depending on the shape and texture of the endosperm and shape of the embryo sac.

(b) Method of food supply.

The configuration of the mature embryo depends on conditions which modify it without acting on it directly, depending on -

(a) the future form of the seedling, itself influenced by the environment;

(b) method of freeing itself from the seed.

(SARGANT 1908).

The/

"The structure of the embryo is dependent on its future as well as on its past". (SARGANT 1914)
 The characters of the young embryo are mainly adaptive: the shape of the whole structure and developmental sequence are more dependent on environment than on ancestral forms. Ancestral forms will be preserved better in the seedling, since the embryo is so plastic. (SARGANT 1908)

2. SIZE OF SEED

The size of seed which is itself related to the reserve food is the determining factor and on it depends the number and size of cotyledonary bundles and therefore the transition phenomena and the number and relative development of hypocotylar bundles. (HILL and DE FRAINE 1913)

TANSLEY and THOMAS in making a scheme for a reduction series based on transition anatomy note the relationship between small seeds and small seedlings, hence small cotyledons and a consequent need for a rapid development of the plumule.

(TANSLEY and THOMAS 1906)

"Given uniform conditions in the seed with respect to the presence or absence of endosperm and perisperm ..., the size of the seedling depends/

depends on the size of the seed"

(COMPTON on Leguminosae 1912)

3. THE SIZE OF SEEDLING limits the scope for evolving new types, but the possibilities are greater in larger seedlings, this possibly on account of physiological demands. (HILL and DE FRAINE 1913)

The size of a seedling then is a factor in deciding its own internal structure according to these authors. "There are many exceptions to the rule that the size of the seedling is correlated with the type of structure." (LEE on Compositae 1914)

4. TYPE OF GERMINATION

In epigeal seedlings in addition to water and food translocation there may be the additional problem of mechanics to complicate the anatomy of the cotyledon. (HILL and DE FRAINE 1913)

"In hypogeal germination, the plumule develops fast". (COMPTON 1914)

5. INFLUENCE OF ENVIRONMENTAL CONDITIONS

The weak development of roots in *Oryza sativa*, and in other aquatic Monocotyledons is due to the habit/

habit. The root development of xerophytes is traced to a similar cause. (KLEBS)

Two sets of factors are continually influencing the seedling, purely physiological factors connected with changes in the environment and those connected with the nature of the organism. So long as the latter set do not unfit the seedling, they will persist. But when they clash with the environment the first set will be brought into play. (LEE on Compositae 1914)

Seedlings are early thrown on their own resources and the struggle for existence transforms the whole structure. (SARGANT 1902)

Primitive characters (in the seedling) are swamped amongst those dependent on external conditions and these are necessarily variable. (SARGANT 1903)

"The struggle for existence between two species in any locality must be profoundly affected by the characters of the seedlings". (SARGANT 1914)

"The more rigorous the conditions the more pronounced the adaptations to them". (SARGANT 1914)

"In Monocotyledons external changes due to habitat would/

would be accompanied by internal changes. The peculiarities in the latter then are the outcome of recent adaptations rather than the expression of developmental history.

(A. W. HILL on *Peperomia* 1906)

6. INFLUENCE OF ADULT STRUCTURE UPON THE EMBRYO AND SEEDLING.

"Neither in ontogeny nor in phylogeny is there sufficient evidence to show that the parts of the embryo are a reduction of those of the adult."

(BAYLEY BALFOUR 1901)

"The structure of the embryo is dependent on its future as well as on its past." (SARGANT 1914)

"A division of the subject (embryology) which excludes the future is purely artificial."

(BAYLEY BALFOUR, quoted by SARGANT, 1914)

"The study of seedling structure has shown the adult habit to have a pronounced influence on the seedling anatomy."

(HILL and DE FRAINE on *Cactaceae* and *Proteaceae* 1912)

BALFOUR considers the limited axial growth of the protocorm/

protocorm to be primary but "the monocotyleous type has developed largely on restricted lines in the way of short rhizomatous, often tuberous growth.

(BALFOUR 1901)

"Habit has influenced evolution, but operating as an ancient differentiating factor. The influence is felt on several families and not in isolated genera and species."

The secondary effect of habit is seen in individuals.

(E. N. THOMAS 1907)

HENSLOW would have it that food storage in a geophilous plant has caused degeneracy of the whole seedling even to suppression of the cotyledon.

(HENSLOW 1911)

"The same type of hypocotylar anatomy occurs in allied species of totally different habit,"

(Gymnosperms and Dicotyledons), but

"Stem structure in the hypocotyl has been acquired in a number of cases in which the hypocotyl projects above ground and early has to support a weight of foliage."

(TANSLEY and THOMAS 1906)

"The initiation of the necessary structural modifications of the adult would begin to be thrown back more and more into the early stages of/
of/

of the plants' development until finally the structure of the embryo itself would become involved." (A. W. HILL on Peperomia 1906)

Suppression of the axis in aquatics (e.g. Pistia) is an adaptation of the embryo to its surroundings. In exceptional forms (e.g. bulbous plants) "causes which result in the suppression of the stem operate more powerfully on the seedling than on the mature plant."

"Correlated with this (the geophilous) habit is deliberate maturation of the embryo". Therefore the plant produces albuminous seeds with small undifferentiated embryos. Strict economy prevails during the first season of growth of the aerial parts. (SARGANT 1908)

"There is an association of the tuberous habit and the reduction of the cotyledonary member." (SARGANT 1914)

"In the morphology of seedlings we find a singular uniformity which contrasts sharply with the uniformity of habit of the mature plant" (COMPTON 1912)

"The/

"The production of large seeds and seedlings is correlated with the tree habit." (COMPTON 1912)

"Local variation in the number of root poles is very commonly found in plants which have a tuberos hypocotyl."

(HILL and DE FRAINE 1913)

As the form of the adult becomes more and more intensified it tends "to work back into earlier and earlier stages in the ontogeny of the successive individuals, until finally a character adaptively acquired by the adults works back into the epicotyl and finally into the embryo."

(GANONG on Cactaceae 1898)

AIMS OF THE PRESENT INVESTIGATION.

1. True comprehension of the seedling is impossible without a knowledge of its anatomy. The present research, therefore, will be justified, apart from other considerations if it enlarges the present boundaries of anatomical knowledge.
2. The extension of previous observations on external features to the internal morphology was naturally kept in mind in the choice of material. In cases where the germination and seedling anatomy of a family had been neglected, special efforts were made to obtain seed.
3. It will be seen that, in the literature on the seedling, most of the evidence on phylogenetic problems was derived from the Liliaceae or from abnormal seedlings e.g. *Arisarum*, *Agapanthus* etc. A wider range therefore would give a better perspective in viewing such work.
4. Previous work on such questions as the relation of the size of seed to that of the seedling and the anatomical features to the general morphology had been confined almost entirely to the Dicotyledons and/

and then limited often to a family (for example COMPTON'S research on Leguminosae). It was believed that if a study of such relationships were made to include a whole phylum and that the Monocotyledons, not only would an interesting comparison with the Dicotyledons be afforded, but a survey sufficiently comprehensive would eliminate individual peculiarities.

5. It was hoped to produce further evidence as far as the Monocotyledons were concerned on the problem of the value of the seedling as an aid to taxonomy and, taking narrower limits, to discover to what extent generic or family affinities were indicated in the seedling.
6. The tendency shown by certain authors has been to multiply the types of germination and cotyledon. A better understanding of both and the possibility of reducing the number of types were a reasonable expectation from this study.
7. The main idea, however, underlying these studies was to find if the habit of the adult plant, itself affected by environmental conditions, impressed itself on the seedling, and if it did so at/

at what stage of development and to what degree. The controversial nature of this aspect of the subject was revealed by the summary of opinions on it.

The data furnished by the examination of the seedlings were arranged so that the plants were reviewed according to family. It was then decided that for the purpose of keeping the above idea clearly before one, a much better classification would be according to habit. There was the further advantage that, as far as is known, this grouping was new, and, therefore, fresh information might be revealed by it.

The difficulties of such an arrangement are obvious. While aquatic and semi-aquatic forms presented no difficulty, other plants of less rigid habit were less easily placed: this applied particularly to members of the rhizomatous group. There were genera which were both climbing in habit and tuberous, or xerophytic and rhizomatous. In such cases the plant was described with members of that section which it most closely resembled. In one instance, however, (that of *Vellozia*) the seedling was placed in the arborescent group, when clearly it ought to have been attached to the xerophytic./

xerophytic. Although certain species of the Commelinaceae are annuals, they differed so little from the rhizomatous type that it was not thought necessary to add a further group of annual plants.

The scheme showed a disadvantage in one respect when the Bromeliaceae were considered for certain genera, (a section of the terrestrial plants), were discussed under the heading of succulent xerophytes, while the remaining seedlings were described in the group for epiphytes.

Since it was thought rather unfortunate that such an exceedingly interesting family as the Bromeliaceae were thus divided, a special summary of the germination and research done on the family has been given, for the sake of unifying the results.

8. Finally there remains to be mentioned the secondary object of this research, namely the collecting of the literature on the subject, as far as its existence was known. An account is given of it here, not chronologically, or even continuously, but with certain sections of it isolated, so that a record of the literature on the seedlings of each family follows the findings of the present writer. In this way a certain co-ordination of past and present/

present work results. A somewhat similar treatment has been accorded to the literature on seedling structure in general so that the views of the same author in the same publication may appear under several headings, as different aspects of the seedling are discussed. This will already have appeared in the preceding pages.

SCOPE OF THE INVESTIGATION.

Families providing material for examination.

Juncagineae	Liliaceae
Palmaceae	Amaryllidaceae
Aroideae	Dioscoreaceae
Eriocaulaceae	Iridaceae
Commelinaceae	Zingiberaceae
Bromeliaceae	Cannaceae
Philydraceae	Aponogetonaceae

Seedlings have been collected, sketched and sectioned for the families Cyperaceae, Haemodoraceae, Juncaceae and Orchidaceae, but a sufficient examination has not been made to warrant their inclusion here. Although the Gramineae are not referred to directly, a certain amount of the literature on this family has been consulted. A register of the seedlings examined and of seedlings mentioned in the literature is given elsewhere.

TERMINOLOGY.

KLEBS' Types refer to those already mentioned and to be found in his publication of 1881.

- (a) The hypocotyl in the present work, is taken to mean/

mean that region having as its upper limit the base of the cotyledon. This level is indicated by the passing of the cotyledon strands to a central position usually to be inserted on the downward continuation of the plumular axis. The lower limit is where the formation of a typical root stele occurs.

- (b) In describing the anatomy SARGANT'S convention of proceeding from the cotyledon to the root has been adhered to, not for any significant reason but because the description is more easily followed. ARBUR (3) has criticised this method as leading to "the fundamental error of treating the root stele as made up of cotyledonary and plumular strands". Its use here is to be understood not as an implication that the root stele is made up of cotyledon and plumular traces, but as the most convenient method.
- (c) The nomenclature as a rule for the parts of the cotyledon is that in general use at present.
- i. "The cotyledon tip" is the portion remaining in the seed.
 - ii. The "stalk" connects the tip to the main portion/

portion of the cotyledon consisting usually of

- iii. A "sheath" extending to the base. This may be extended upwards into a hollow tube of varying length, termed "the ligule".

In certain cases the portion connecting sheath and tip is flat and leaf-like (Fig.). In such instances this region is referred to not as a stalk but as a lamina, and its downward prolongation, usually narrow, as a "petiole". The word "lamina" has also been applied by the writer to the cylindrical, green portion of the cotyledon appearing above ground in epigeal germination, since no suitable term in common use could be found.

MATERIAL

In the great majority of cases, seeds were collected from plants growing in the Royal Botanic Garden, Edinburgh. In some instances they were obtained from continental centres and from South Africa.

The research was made possible by having at one's disposal the wealth of material growing in the Garden. The writer wishes to record her indebtedness to Professor W. Wright Smith, Regius Keeper of the Royal Botanic Garden, and his University and Garden staff. In particular she desires to acknowledge the assistance rendered by the staff of the Propagating Department under Mr. L. B. Stewart, who germinated all the seeds and raised all the seedlings.

METHODS

Germination of Seeds.

The seeds were collected for the most part from plants growing in the Royal Botanic Garden, Edinburgh, but in some cases were sent from centres in Europe and even further afield. They were sown in pots, and in a few instances on moist blotting paper; seedlings being collected at stages from a day to several weeks/

weeks old. In isolated cases, observations were continued for one or two years.

Fixation of Seedlings.

Carnoy's Reagent proved a suitable solution for this purpose, the seedlings remaining in this for half an hour.

Imbedding, Sectioning and Staining of Material.


The seedlings, after being washed in absolute alcohol, were preserved in 75% alcohol containing a trace of glycerine. After dehydration they were transferred gradually to pure chloroform, (this taking from two to three days) in which they were immersed from twelve to twenty-four hours, paraffin wax of a medium hardness (M.P. 50°) being added gradually in the cold. After twelve—twenty-four hours in the chloroform-paraffin mixture, the chloroform was allowed to evaporate and the seedlings, after remaining in paraffin at 51° for a period varying from one to three days, were imbedded.

Chloroform was used as a solvent in preference to xylol as being more easily detected if present before the actual imbedding. The length of time taken for penetration of chloroform and later, paraffin, was compensated for by certainty of results, the early attempts/

attempts at imbedding with xylol as solvent, and three or four hours as the interval of time between different stages of the process, having proved unsuccessful.

A thickness of 10μ was chosen for serial sections which were made longitudinally and transversely, for each stage of development examined. Sections were stained with a solution of 1% Safranin in water and 1% Safranin in alcohol and counterstained with 1% light green in clove oil. This proved to be a very satisfactory combination.

The number of genera examined was
This included ——— species.



2. DESCRIPTION OF SEEDLINGS, CLASSIFIED

ACCORDING TO

THE HABIT OF THE ADULT PLANT.

H Y D R O P H Y T E SAPONOGETONACEAEAPONOGETON ABECESSINUS

Four seeds and four seedlings were examined.

Seed - non-endospermic. The ripe ovules occur in groups of three per carpel, being easily seen through the transparent walls of the latter.

Embryo - straight, spindle-shaped and 1 mm. long at maturity. It is protected by an outer delicate, transparent and an inner reddish-brown seed coat. Sectioned longitudinally (Fig. 1) it shows a clearly differentiated primary root with a prominent root cap, lying opposite the micropyle. The plumular bud develops laterally just above the radicle. The second and third foliage leaves may be differentiated before germination. The bulk of the embryo consists of cotyledon, the closely packed cells of which are filled with small elliptical starch grains. A single vascular strand, of undifferentiated meristem, runs centrally down the cotyledon to the primary root. It is joined by a very weak trace from the plumule.

Germination. The radicle emerges through the micropyle and a ring of root hairs arises on a collar of tissue, /

tissue, immediately behind the root tip and below the level where the plumule is placed. An adventitious root makes its appearance above the root hairs and keeps pace in development with the plumule, doubtless as a balancing organ. The cotyledon does not become erect; it consists for the most part of a ribbon-like blade, connecting tip and short sheathing base but is originally cylindrical. It maintains a position with the tip and much of the "blade" underground, possibly for still better anchorage than the primary root and its first adventitious root (on the side remote from the cotyledon) afford. The primary root continues to elongate for some time. At the end of four or five weeks a small spherical corm-like body has developed at the base of the shoot region, an indication doubtless of the "sympodial growth and tuberous stem (3) characterising the family Aponogetonaceae". (Fig. 1)

Anatomy

(i) Seedling a few days old.

- (a) Cotyledon. This is, at first, cylindrical with a simple vascular strand, enclosed in a thin-walled sheath, running through it centrally. This strand lies in a tissue of closely/

closely packed cells, placed between two aerenchymatous regions. In older seedlings, the cotyledon is a flattened structure of the isobilateral equitant type with aerenchyma occupying a larger volume of the leaf. Although the stele of the cotyledon strand does not increase in size or complexity to any extent, in the sheath it shows a marked development of thickening on the inner tangential walls.

- (b) First Leaf. It resembles the cotyledon in shape and in the distribution of aerenchyma but has two lateral strands in addition to the mid rib.
- (c) Transition. The traces from the plumular bud and first foliage leaf resolve themselves into a central and two lateral groups. These are joined by the cotyledon strand, a triarch arrangement resulting. At the root hair region, the root becomes diarch; lower, the xylem is reduced to a single element. Aerenchyma appears in three or more patches in the cortex.

- (ii) Four weeks old Seedling (Fig. 1) Sections, taken through the corm-like body already referred to/

to, show

- (1) at the upper limit merely a section through the plumular bud surrounded by the bases of four leaves and the remains of the base of the cotyledon,
- (2) a region where the strands from the latter pass in close succession into a central solid axis. Adventitious roots originate at this level.
- (3) a much swollen hypocotylar region consisting of a ground tissue of large starch-storing parenchyma protected by an outer covering of two or three layers of regular periderm cells. This swollen body is traversed by stout vascular strands from which five or six rootlets run out.

The rootlets are of the same type as the primary root with a simple stele, consisting of a central xylem element enclosed by a ring of phloem and parenchyma, and an endodermal sheath with thickened outer and radial walls. The cortical cells are large, thin-walled and loosely arranged.

ARBUR (3) refers to the food storage in the cotyledon and figures two stages in germination. She draws attention in particular to the/

the sheathing base of the cotyledon which, in older seedlings, is prolonged into two "sheath-wings" about the plumular bud. This feature will again be referred to in discussing in general the morphology of the cotyledon.

J U N C A G I N A C E A E

TRIGLOCHIN MARITIMUM

Six seedlings were examined.

Seeds were obtained from plants growing in Aberlady Salt Marsh but only two germinated. Accordingly, seedlings were collected from the Marsh in the following spring.

Seed - has three faces and a golden-yellow testa, and is 4 mm. long. T. G. HILL (63) who describes the embryology as far as the production of the mature embryo though not the germination, and discusses the anatomy of the adult, remarks that "the mature embryo is straight and not curved as in *Alisma*". The ripe seed is exalbuminous, the bulk of the seed being occupied by the cotyledon: the primary root is a blunt organ at one end with the plumular bud occurring/

occurring laterally, immediately above it.

SCHLICKUM comments on the short, thick hypocotyl, weak radicle, the initial of the vascular strand of the cotyledon, and the food reserve, which is starch and aleurone with a few large drops of oil. The second foliage leaf is differentiated before germination.

Germination. SCHLICKUM (109), in his research on the relation between the cotyledon and first leaf, made a careful study of the germination of *T. Barrelieri* and *T. maritimum*. His findings with regard to the development and the anatomy of the two organs are exactly the same as those of the present investigation on *T. maritimum*.

The primary root, represented by a short blunt cone surmounted by a swollen collar, is pushed out of the seed by the elongation of the cotyledon. Very young seedlings are devoid of root hairs, but when the cotyledon becomes erect a ring of these arise from the swelling. Although the radicle is so weak initially, yet by the time the first two leaves have appeared it has become relatively long. (Fig. 3)

Longitudinal sections of the early stages show that the bulk of the seedling is cotyledon, which is/

is at first cylindrical, and later made up of an open sheath, and narrow lamina, with little differentiation in the suctorial portion. The plumule appears through a slit towards the base of the cotyledon and develops slowly. Intravaginal squamules (T. G. HILL'S "sessile glands") occur from the first, even in the axil of the cotyledon (noted also by SCHLICKUM who calls them "adventitious buds"). The cotyledon gradually dies back, the sheath itself becoming partially destroyed by the growth of adventitious roots through it.

Anatomy.

- (a) Cotyledon. In the young seedling the cells of the suctorial tip contain no starch but the free part of the cotyledon is rich in food stuff, viz:- starch, oil, aleurone (3). The epidermis has a thickened outer wall, is made of medium sized cells enclosing a ground mass of five - six rows of parenchyma with large intercellular spaces, the outer layers containing chlorophyll (Fig. 3). Towards the base a hollow appears on one side and the outline seen in transverse section, is crescent-like, enclosing the plumular bud, meristem of first foliage leaf and a squamule./

squamule. The epidermis of the sheath on the upper side has larger cells and outer walls more thickened than on the lower epidermis. Stomata occur, though not found by SCHLICKUM. There is also spongy tissue towards the centre. LEWIN found one or three strands proceeding through the cotyledon; SCHLICKUM pointed out that in those cases where three were found, LEWIN had probably mistaken the first leaf for the cotyledon, the latter being already dead. My sections bear out SCHLICKUM'S remarks, for in no case did the cotyledon possess more than one strand. This strand (Fig. 3) is collateral, being made up of a single phloem mass adjoining an equally well developed patch of phloem, the whole surrounded by a well defined sheath of small cells. It runs centrally through the cotyledon, its course being diverted temporarily above the plumular mass with which it fuses. Hypocotyl is practically absent.

- (b) The primary root (Fig. 5) with wide cortex and small simple stele is 2-arch, with a pith throughout most of its length; this is interesting in view of VAN TIEGHEM'S contention that the xylem strands/

strands do not meet in the centre but are separated by parenchyma, an observation which is questioned by HILL. The pericyclic cells are as large as those of the endodermis, which is thickened on the radial and outer walls. There is a hypodermal layer which stains like the epidermis and evidently corresponds to the exodermis behind the piliferous layer, which is described by HILL for the adult adventitious roots.

Longitudinal sectioning of a seedling two or three days old (Fig. 4) shows in addition the collar of cells from which the root hairs originate. The collar effect is produced not by additional layers of cells but to the nature of the cells which are much enlarged. They are roughly rectangular in outline and strongly meristematic. Material was not procured of such an age as to show the initiation of a rhizome. The adult adventitious roots are six or seven arch with wide lacunae in the older roots (HILL, 63).

- (c) First leaf. The radial symmetry, epidermis, assimilation, parenchyma and ground tissue with large intercellular spaces are as in the cotyledon. Three strands of the same nature as the cotyledon/

cotyledon bundle, run through the blade and unite at the tip. At the base the central one is the strongest (SCHLICKUM). The second leaf is similar but with photosynthetic tissue better represented, and succeeding leaves are of the same type save for the fact that their sheaths remain colourless and serve as storage organs for starch (109). HILL mentions that air spaces, schizogenous in origin, occur in the leaves of the adult plant.

ERIOCAULACEAEERIOCAULON SP.

The seed, which came originally from Assam, was obtained from Kew. Unfortunately the initial stages of germination were not observed and attempts to get seedlings of the native *E. septangulare* were unsuccessful. HOLM (70) in 1901 commented on the paucity of publications on the anatomy of *Eriocaulon* which, although possessing some characters in common with other Monocotyledons, had several peculiarities, for example the unique inflorescence and floral structure, peculiar habit and distinctive morphological characters. RUHLAND in his description of the Eriocaulaceae also remarks on the highly noteworthy features in the internal anatomy of the vegetative organs. How far the seedling resembles the adult *Eriocaulon* and the seedlings of other aquatics dealt with, will now be seen.

The fruit is produced from a trilocular ovary, with one elliptical seed per locule. The seed is covered with a testa of two layers of cells, the inner coloured yellow or red-brown ().

Embryo - very small and lentiform, lying opposite the hilum/

hilum. The cells of the endosperm are filled with very small starch grains.

Germination (Fig. 9). According to RUHLAND, who gives a brief account of the germination of *E. Ulaei*, this offers no point of special interest. It is evidently of the same type as *Triglochin* and *Aponogeton*. The embryo having emerged from the seed by pushing off the micropylar lid, development of both plumule and radicle is very slow. The tap root is supplemented early by numerous strong adventitious roots: in a seedling a few weeks old the primary root has already been replaced by the latter. From personal observations, it appears that the cotyledon never assumes a vertical position, but remains with its tip fixed in the soil as an anchoring agent. The adventitious roots arranged in a ring are also an effective means of fixation. The leaves are arranged in close succession on a short stoutish axis and are long and very sharply pointed. Between the leaves there arise long unbranched multicellular hairs in a tufted fashion. Their origin seems to be the base of the leaf at its insertion on the axis.

Anatomy of seedling. No literature found on this subject.

(a) Cotyledon/



- (a) Cotyledon - this is linear and throughout the upper part of its length is almost cylindrical. Towards the base it becomes more flattened. There is a single vascular strand of a simple nature (Fig. 8) enclosed in a remarkably strong sheath of seven - nine thickened cells, the larger towards the outer surface. This sheath is itself surrounded by a ring of very large cortical cells with thin walls. Two large air cavities occur on each side of the vascular strand, bridged over by star shaped chlorenchyma, occurring as diaphragms. The abaxial surface consists of only one layer of cells. The opposite surface is made up of an epidermal layer of large parenchyma, rectangular in transverse section, and one hypodermal layer. Upper and lower epidermis are thinly cutinised.
- (b) First foliage leaf (Fig. 8,9). In their linear shape and lack of sheathing base as well as in internal features, there is a close resemblance between cotyledon and first leaf. The tissue of the first leaf has two large air spaces on either side of the midrib which, like the cotyledon strand, has a simple stelar structure and a double sheath. In addition there is a pair of lateral/

lateral strands. RUHLAND (101) refers to the same internal fenestration in the early leaves of *E. Ulaei*. In every feature there is a close similarity to the leaves of *E. decangulare*, a plant of sphagnum swamps studied by T. HOLM. He describes a leaf which is linear, without a sheath, nearly flat, or with margins somewhat involute, with a large-celled, thinly cutinised epidermis on both surfaces, the upper having especially large cells (cf. cotyledon); hairs occur on both sides of the blade. Between each two mestome bundles the mesophyll is broken down into wide lacunes with diaphragms of star-shaped cells (Fig. 9). "Around each mestome bundle is a sheath, which at first glance was considered identical with the parenchyma sheath as seen in many genera of other orders" - none such was found in the stem, and in longitudinal section of the leaf the cells were indistinguishable from a collenchyma sheath. Another sheath occurs within the first, thicker walled than the outer. In POULSEN'S opinion (92) the outer one would represent true parenchyma, the inner one schlerenchyma. HOLM remarks in the conclusion of his paper that the leaf is "not much different from/

"from that of *Cyperus*, *Kyllingia* etc." ARBUR figures a mature leaf of *E. septangulare* (Fig. -), which evidently repeats the foregoing features.

- (c) Transition (Fig. 9). The plumular traces in a young seedling reduce to five which fuse further giving a central group of metaxylem with two protoxylem groups on one side and two phloem groups on the other. The cotyledonary strand passes in towards the centre and joins them forming a single bundle. Thus plumule and cotyledon contribute to the root stele which is of a very simple nature, being diarch. The xylem and phloem are reduced to a few elements, surrounded by a powerful pericycle of six or seven cells thickened in some cases on all four walls, in others on the outer tangential wall only or on this and the radial walls. The endodermis is composed of nine or ten larger cells with thickening laid down on all walls though more thinly on the outer tangential walls. The cortical cells are large and thin-walled, the epidermal cells regular, large and with a thin coating of cuticle.

The young adventitious roots (Fig. 7) which/

which early replace the primary root repeat the above features, save that the pericycle though still consisting of large conspicuous cells is unthickened, while the thickening of the endodermis is hardly perceptible. The cortex is so delicate that it tends to break down on sectioning. Most steles contain only two metaxylem elements.

At later stages the adventitious roots are polyarch and aerenchymatous (\triangle). HOLM found wide lacunes in the cortex of *E. decangulare* and the horizontally placed diaphragms at intervals; there is no hypoderm and here as in the species described above, the endodermis is thin-walled, therefore he classes such roots as "simply nutritive since they possess no pronounced power of resistance and are not contractile or especially adapted for storage". In the adult *E. decangulare* the epidermis of the short rhizome (one-two inches long) is developed into long hairs.

Several points of interest arise from the foregoing study:-

- (a) The striking resemblance between the cotyledon and first foliage leaf not only in external/

external morphological features but in disposition and nature of the internal tissue, including epidermal layers, aerenchyma and sheaths surrounding the mid-rib.

- (b) The similarity to other aquatics studied. This will be referred to in a general discussion of the group.
- (c) The sheath of schlerenchyma surrounding the cotyledonary strand, and the outer parenchyma sheath.
- (d) The fact that different species of *Eriocaulon* show exactly the same peculiar anatomical features and that there is little or no divergence in vegetative characters in the primary root.
- (e) The unusually strong pericyclic development finds a parallel in certain of the Bromeliaceae, a closely connected group, phylogenetically; the sheath of the cotyledon strand in *Eriocaulon* recalls that of *Philydrum*, a related genus.

P H I L Y D R A C E A EPHILYDRUM LANUGINOSUM

The family Philydraceae is made up of three genera; of these, Philydrum is monotypic. Six seedlings were examined. Seed was obtained from the Botanic Garden at Munich.

The ripe seed is 0.5 mm. long, spindle-shaped, with peg-like outgrowths on the outer seed coat, possibly for anchoring purposes. In some illustrations (Fig. X) the testa seems to be thickened by spiral bands but none of the seeds examined personally, showed this feature. The seed is non-endospermic at germination. The embryo is straight.

Germination (Fig. X). There is no noteworthy feature: resembles that of Triglochin, Eriocaulon and Aponogeton. The cotyledon consists of very short base, long linear petiole and very short tip. The primary root is at first a short blunt tip protected by a flattened root cap. The plumular bud arises immediately above the primary root: its position is indicated by a swelling merging into the primary root. The first leaf, the only one differentiated at germination, emerges, as in the preceding genera, by a lateral/

lateral slit and the cotyledon straightens out, vertically, carrying the seed coat on its tip. Even in the youngest seedling a ring of adventitious roots and root hairs develop above the root cap. The primary root elongates below this short hypocotylar region and for some time is the principal root. When the seedling has two or more foliage leaves, the radicle is reinforced by stout adventitious roots arranged round the flattened base of the axis, which has increased considerably in girth (diam. more than 1 mm.). The leaves are isobilateral equitant, rising in close succession.

Anatomy

- (a) Cotyledon (Fig. 11). In the early stages the single vascular strand proceeds from the cotyledon tip to the primary root, its course being vertical save where it is made to deviate by the plumular bud; the contribution of the latter to the radicle being almost negligible. The cotyledon strand is simple. It is composed of four xylem elements and a small phloem group enclosed by a sheath of very large cells, thickened after the fashion of an endodermis and closely resembling the sheath of the cotyledon in *Eriocaulon* sp. The tissues of the cotyledon are/

are similar in their nature and arrangement to those of genera already described, that is to say, at levels towards the basal sheath the cotyledon presents, in cross section, a crescent with two wide lacunae, on each side of the centrally placed vascular strand. Large cells, thinly cutinised, comprise the upper and lower epidermis. The mesophyll as seen in longitudinal and transverse section, is reduced to two layers of chlorenchymatous tissue, loosely arranged. The young cotyledon has radial symmetry.

- (b) The primary root (Fig. 11) is exceedingly simple, anatomically, doubtless on account of its supply from a solitary cotyledon strand. There is an epidermis of large, regular cells, a cortex four or five layers deep and a small stele with a prominent endodermis of six or more large cells thickened on all but the inner tangential wall. The xylem tract is merely a group of four elements; there is an equal bulk of phloem and practically no parenchyma.
- (c) The first leaf (Fig. 12). At first symmetrical provided with a mid-rib and a trace of meristem for/

for two lateral strands. The epidermal cells are large with clear contents and the mesophyll two or three layers deep. In an older seedling, it has developed long and wide lacunae between its mid-rib and the two lateral strands, exactly as in *Eriocaulon*.

A R A C E A E

PISTIA STRATIOTES. (Fig. 12)

Longitudinal sections were made of the young seedling, but unfortunately lack of material prevented a more thorough investigation being made.

The suppression of the Primary Root, early origin of numerous adventitious roots, and short thick axis are obvious from the sections. The cotyledon, which is aerenchymatous, acts as a float from the time of germination.

According to SARGANT (105) the suppression of the axis in the embryo of the plant is an adaptation to its surroundings for a stem is a feature of the mature plant.

HEGELMAIER'S diagram of the ripe embryo is reproduced. (Fig. 12).

LITERATURE

The literature on the germination and seedlings of monocotyledonous aquatics is concerned chiefly with description of general morphology, no attempt being made to correlate anatomical features of different genera. HEGELMEISTER (58), and KOCH (81), describe the development of the embryo and germination of *Pistia Stratiotes*. HANSTEIN (57) gives an account of the embryo of *Alisma Plantago*. Observations on the seedling with some anatomical details are given by IRMISCH (76) and KLINSMANN (134) for *Stratiotes aloides* and *Najas major*, the germination of the former being included in LUBBOCK'S types of seedling. *Stratiotes* agrees with the seedlings which I have examined in its habit, e.g. shape of cotyledon and well developed plumule. There is no trace of radicle but the hypocotyl is of considerable bulk. Anatomically simple, the embryonic plant is provided with a single cotyledon strand, whereas the first leaf has a mid-rib and in addition one or two pairs of laterals.

Halophila and *Thalassia*, two interesting marine types, are mentioned by LUBBOCK as being also macropodous with well differentiated plumule. The former/

former is described in great detail by Professor Bayley Balfour: the cotyledon has a single vascular strand whereas the first leaf (not necessarily a true foliage leaf, however) has a main and two lateral strands. There is no radicle and, probably, no foliage leaves in the ripe embryo; but an enormous development of hypocotyl has occurred.

The mature embryo for a series of P was examined by D. H. CAMPBELL in order to discover its value phylogenetically: for example, he draws a comparison between Sparganium, Gramineae and Aroids, none of which have a suspensor although each has a very good development of endosperm. Sparganium, he notes, consists chiefly of cotyledon; Najas has half the bulk of the embryo given up to the cotyledon, and has intercellular spaces in the root, even before germination, Zannichellia has a primary root proportionately larger than that of either, the result of a greater contribution from the young embryo in its initial development. The three have in common then, an embryo with plumule highly differentiated at maturity, a dominance of cotyledon, and poverty of primary root. SCHLICKUM describes in detail the anatomy of the young seedling of Alisma Plantago, which was figured by KLEBS and LUBBOCK and studied by TSCHIRCH/

TSCHIRCH (126) and VAN TIEGHEM (136). It is characterised by those features which ARBUR (2) notes for the majority of aquatics, namely, a primary root which elongates some days after germination, although inconspicuous at first, a ring of numerous root hairs, a cotyledon with filiform blade and open sheath and simple internal anatomy. The cotyledon possesses a single vascular strand of a few xylem elements and sieve tubes, while the three leaves first formed have a central and two lateral strands (later leaves differ in shape from these).

DISCUSSION

In discussing "The Ecology of Water Plants", ARBUR (2) uses the expression "biological group", and defines ecology as "the study of the relation of plants to their habitats, of their different forms of association with one another and of their applied physiology in general". The question therefore arises - how far would a survey of seedlings of aquatics, apart from all knowledge or consideration of the adult, reveal that in them one was dealing with a/

a "biological group"?

- (a) In KLEBS'S classification, Group VI. is the most satisfactory one in that the seedlings behave in a consistent fashion regarding absence of endosperm, type of germination (epigeal), development of primary root, and production of a garland of strong root hairs. They are all aquatic or marsh plants, and KLEBS puts forward reasons for their unusual features.
- (b) It can hardly have been mere coincidence that SCHLICKUM (109) chose three genera which were aquatic and which show striking resemblances to one another in collecting evidence for his comparison of the cotyledon with the first leaf in monocotyledonous seedlings.
- (c) Writing of the adult form of aquatics, ARBET remarks that "fundamental changes in habit are necessarily associated with marked divergences from the structure and life history of land plants" (p.3 "Water Plants"), but adds (Ch. XIX) that the "germination and development of the seedling in aquatics vary according to the natural affinities of the plants in question, and are characterised by few peculiarities related/

"related to the environment, except a very frequent reduction of the primary root". She mentions the reduced or non-existent radicle in some, the anchorage by root hairs in those requiring this, the absence of endosperm and macropodous embryo in the Heliobieae and factors necessitating food storage in the hypocotyl in the latter group. Here already are more than a few peculiarities: there is indeed an indication in gross morphology alone of the marked divergences from a normal seedling of a geophytic type, corresponding to those changes which she records for the adult. In discussing the aerating system of stems, leaves and roots of water plants, (Ch. XX), ARBER notes that this is developed with a uniformity and an elaboration in plants belonging to the most divergent cycles of affinity, an undoubted indication of the influence of the milieu. We should expect the seedlings then to show uniformity along lines similar to the adult as a result of the habitat. Surveying the group of plants examined in the present research the following points of similarity are discovered:-

(a) Type of germination and rate of development.

(b)/

- (b) Nature of the cotyledon, which in all cases is assimilatory and in a few cases is later a balancing organ. An open shallow sheath merges gradually into a flattened, then cylindrical "lamina", which tapers to the suctorial tip.
- (c) Nature of the first, second and third leaves, which, like the cotyledon are noteworthy for their simplicity of shape and structure; early differentiation and strong development of plumule.
- (d) Similarity between cotyledon and first leaf in general morphological features.
- (e) Nature and behaviour of the radicle which at germination is always poorly developed but which may grow at a later stage.
- (f) Presence of the garland of stout root hairs.
- (g) Early appearance of adventitious roots (a feature by no means confined to aquatics).
- (h) Uniformity in "habit" of the young plant with/

with the leaves arising in close succession on a short axis, giving a squat appearance.

- (i) Similarity in anatomical features. ARBUR remarks (Ch. XXVI) that "Structural reduction is one of the most marked characteristics of water plants." In the vascular skeleton of the seedlings there is the utmost simplicity as to the course of strands and economy of material.

In all cases considered, including those recorded in the literature, the cotyledon is traversed centrally by one simple vascular strand and the radicle has a stele with only a few conducting elements, in marked contradistinction to those of seedlings of other ecological groups. The first leaf repeats the features of the cotyledon but in addition to the mid-rib is provided with a pair of weak lateral strands (133, IRMISCH, records two pairs in some cases for Stratiotes): instead of being cylindrical it is usually flattened, and, naturally, has more assimilatory tissue.

The presence of strong sheaths round cotyledon and root strands is interesting and the similarity/

similarity of distribution as well as the very early appearance of aerenchyma (it is to be found frequently in the ripe embryo - e.g. *Aponogeton*, *Najas*).

It has been pointed out frequently (2, 105, 18, 8) that Alismaceae were probably the nearest approach to ancestral Ranalean stock. Are the features in seedling structure which aquatics of other families share with *Alisma* to be regarded as primitive? It is taken for granted that such aquatics are the descendants of terrestrial ancestors which have reverted to a remote ancestral habit. The simple cotyledon strand is to be regarded then not as a case of primitiveness but as another case of extreme reduction, in genera which at one time were adapted to life on land. Thus the single cotyledon strand is found in certain of that group of highly specialised xerophytes the Bromeliaceae. The cotyledon strand of *Eriocaulon* bears a striking resemblance to those in Bromeliaceae, to support this argument. There is no better illustration of the "Law of Loss" in evolution than that provided by the poverty of development of the primary root of aquatics, /

aquatics, which produce perforce their ring of root hairs to carry out the work of a radicle. One has only to contrast this root system with that of the seedlings, the habitat of which provides conditions of a totally dissimilar character, viz., complete xerophily, to realise that environment in the case of hydrophytes has profoundly modified the seedling.

ARBUR looks on the macropodous embryo as possibly not the result of aquatic life but rather a factor favouring it. This point of view might be adopted in considering the seedling in general, which, on account of certain features or a happy combination of these, has been found suitable for the peculiar conditions which the habit of the adult has forced upon it.

MARKEDLY XEROPHYTIC TYPES(A) SHOWING SUCCULENCE

Seedlings from two genera of the Liliaceae (both of the tribe Aloineae) from one of the Amaryllidaceae, and two genera of Bromeliaceae, were examined.

LILIACEAEALOE (Figs. 13-15).

Nine species provided seedlings for examination, two or three specimens from each being sectioned. The seed of some species was brought from South Africa in 1928, and in a few cases the plants are not yet named.

Seed - irregular in shape; three- or four-sided, four-seven mm. long.

Embryo - cylindrical, straight, lying in the middle of endosperm.

Germination - Type I (KLEBS). Development fairly rapid at first; a seedling a week old shows the first leaf 3-6 mm. long. The seed remains at, or a little below soil level. The endosperm has all been used up at the time of germination, but the seed adheres to the cotyledon tip until it rots. The first leaf emerges/

emerges by piercing the apex of the cotyledonary sheath.

Seedling - noteworthy points are:-

- (i) Extreme succulence of cotyledon, first leaf and, to a less degree, radicle.
- (ii) Dominance of first leaf from time of its emergence.
- (iii) Slow development of succeeding leaves and short internodes.
- (iv) First leaf seems to be of same nature as adult leaves in shape and in occurrence of marginal teeth, (A. Davyana), silica granules (Fig. 13) raphides, etc.
- (v) The extremely efficient protection of the plumular bud in a hollow, scooped out at the base of the youngest leaf, so that it is nowhere exposed. The youngest leaf is itself completely ensheathed by the next oldest leaf, in the same manner.
- (vi) In the species examined there is a fair uniformity in size discrepancies being due to differences in shape and length of first leaf. Throughout there is the same type of germination, smallness of seed, sparsity of endosperm.

Anatomy/

Anatomy.

(a) Cotyledon - consists almost entirely of water-storing cells. It is less succulent as the seedling ages. Two cotyledonary strands follow a parallel course, though the suctorial tip may have a double bundle instead of two single strands (*A. parvispina*). The cells of the hood-like "ligule" become attenuated on the side remote from the seed in order to keep pace with the first leaf. In all species, the sheath is the principal part of the cotyledon. In seven species, viz. *A. plicatilis*, *striata*, *verracunda*, *variegata*, *Davyana* and *K. 97*, the sheath joins the suctorial tip abruptly, but in *A. arborea* there is an attempt at a connecting stalk while in *A. parvispina* a stalk 1.5 mm. in length, and assuming an almost vertical position can be distinguished. In *A. Davyana* the seed is connected to the top of the sheath, i.e. the "ligule" is missing.

(b) Transition - according to Sargent follows Type III. The cotyledon strands enter the central axis at different levels before the transition.

(c) Primary/

(c) Primary Root. In the species examined it varies -

- (i) in thickness. Although the stele of *A. Davyana* is the weakest, the root has the greatest diameter, due to a water-storing cortex.
- (ii) anatomically; it may be 4-arch, as in *A. parvispina*, *Davyana*, *plicatilis*, *striata*, K. 97; 2-arch, as in *A. arborea*; or 6-arch as in *A. variegata*.

The primary root is persistent, but is reinforced by cauline roots when the second and third leaves develop. In *A. variegata* an exodermis immediately below the piliferous layer is thickened on the outer walls and stains with phoroglucin and also with Sudan III, though here and there thin-walled cells are placed. This feature is found in *A. parvispina*, *striata* and *Davyana*. *A. plicatilis* possesses such an exodermis. The endodermal layer has thickening on tangential as well as radial walls with cells entirely free from thickening, at intervals. Except in *A. parvispina* and *A. variegata* the rays of the root stele are peripherally placed, not meeting in the centre (ENGLER notes this for the/

the adult plant). But the first cauline root of *A. parvispina*, is 6-arch with this scattered peripheral arrangement. In *A. striata* the 4-arch primary stele tends to have centrally placed strands but they are peripheral in cauline roots where there are six-seven strands. One seedling of *A. striata* was 5-arch, but the commonest type was 4-arch.

- (d) First Leaf - three-five strands arranged peripherally. (Six in *A. plicatilis* which was the longest leaf in seedlings of same age and different species.)
- (e) Second Leaf - similar in shape to first leaf (possessing six main and six subsidiary strands in *A. plicatilis*). The leaves of *A. Davyana* were very thick and rigid.

The only literature found, on the above genus, concerning the seedling was SARGANT'S (103) note on six species; and ENGLER'S (37) sketches of a few early stages with no anatomy except for the adult. SARGANT classes *Aloe* with the arborescent type but the seedlings show little affinity with the latter as will be seen when this group is discussed in the following pages./

pages. She comments on the very short transition and claims that the root depends solely on the three or four plumular traces for its symmetry, evidently on the grounds that the cotyledon traces are inserted on the plumular traces before or at the transition. But the instances in which this arrangement occurs, are numerous and in few of them would this argument hold. As can be seen, especially in longitudinal sections, the traces from the cotyledon play a considerable part in the constitution of the primary root.

Note: The upward prolongation of the cotyledon is not a true ligule, though certain authors would term it so.

GASTERIA VERRUCOSA

Two seedlings were studied.

Seedling - resembles Aloe in

- (i) succulence of whole seedling;
- (ii) cotyledon - short, succulent; function chiefly sheathing;
- (iii) course of two strands in cotyledon;
- (iv) short, thick, persistent primary root;
- (v) type of germination and rate of development;
- (vi) very well protected plumular bud, short internodes, absence of hypocotyl;
- (vii)/

- (vii) relative proportion of first leaf, plumule, cotyledon and root in seedlings of the same age.

Anatomy

- (a) Cotyledon. Two strands follow parallel courses from tip to the top of the sheath, "ligule" and stalk being absent. Here the strands diverge a little, the upper continuing horizontally before assuming a vertical direction downwards. At the base of the sheath they both join the plumular traces at the same level (these traces are chiefly from mid-rib of first leaf).
- (b) Transition. A triangular plate results. Almost immediately (50-60 μ lower) it rearranges itself into chains of xylem which are resolved into a 2-arch root stele which therefore comprises elements from plumule, first leaf and cotyledon. The primary root is a water storage organ, huge cortical cells being concerned with this.
- (c) First leaf - so succulent as to be practically cylindrical at base. The sheathing base is very short but extremely effective. The vascular supply, consisting of a mid-rib and two/

two lateral strands in marginal positions, is poorly developed.

B R O M E L I A C E A E

DYCKIA FLORIBUNDA

Eight seedlings examined.

Seed. A membranous outer integument provides a wing for the flat seed. It soon rots. The endosperm is an ovoid mass 3 mm. long.

Embryo. In ripe seed well differentiated, occupying a lateral position and consisting in the main of cotyledon, with well marked strand, terminating in broad, capped radicle opposite the narrow end of the seed. Hypocotyl is non-existent. The first leaf rudiments are clearly separated from the cotyledon tissue and the cotyledon is already provided with a slit for the emergence of plumule.

Germination and Description of Seedling (Fig. 16).

A day old seedling is 4-5 mm. long. The lowermost $\frac{1}{2}$ mm. is covered with an extremely effective root hair system, very tenacious of soil particles, making it difficult to clean. The region extending $1\frac{1}{2}$ mm. above/

above this is smooth and transparent. The remaining part, cotyledon, is broad with the seed attached to the extremity, which is bent at right angles to the axis. The cotyledon is deeply slitted at the side nearest the seed; this lateral rupture is indeed more than a mere slit, for it results in the gradual unfolding of the cotyledon and expansion of its wide photo-synthetic blade, within six weeks or so: here we have an effective compromise between a cotyledon entirely sheathing and one taking on the functions of a foliage leaf. Development is slow, in spite of the fact that the young plant is so completely differentiated into its parts.

A six weeks old seedling - is little larger being 6 mm. or so, in height, but bulky. The appearance of sturdiness is really produced by the dominance of the cotyledon, consisting as it does now, of

- (i) suctorial tip, a blunt stopper, occupying not more than one-third of seed;
- (ii) long, wide lamina, tapering upwards into tip, downwards into
- (iii) sheath, comparatively short.

The root is still a small fraction of the total length but having a dense mass of root hairs.

Eleven/

Eleven weeks old seedling. There is now a marked difference in the symmetry of the plant which shows the beginning of a rosette. The first leaf is the same size as the cotyledon and opposite to it. The remains of the seed still adhere to the tip of the seed leaf. The radicle, 7 mm. long exceeds the aerial portion of the plant in length and is reinforced by an adventitious root which buttresses rather than acting as a normal root. The first and succeeding leaves possess marginal teeth.

Four months old seedling. Few new features have appeared. The fourth leaf appears in the rosette between the position of the second and third leaf. The tendency for a squat type of plant, with cotyledon, first and subsequent foliage leaves spread out (thus making for good equilibrium) is now marked. The radicle has not increased in length to any extent; the one cauline root is double the length of the primary root and sends out lateral rootlets at regular intervals.

Seven months old seedling. Of seven seedlings of this age, each possessed only one cauline root of 15-22 mm., and a primary root of the same length as the/

the plant at the eleven weeks old stage. Root hairs covered every part of it. The cotyledon had shrivelled and the fifth leaf was in an advanced stage of development.

Anatomy. The single cotyledon strand proceeds from the tip to the base of the cotyledon sheath, acting as a mid-rib to the massive, succulent, leafy body. There is no obvious "doubleness"; the bundle is a simple collateral one made up of xylem, phloem, and parenchyma, enclosed by a sheath, the mesophyll of the blade differs in no way from those cells in the cortex of the hypocotyl.

The first foliage leaf - is supplied with a mid-rib and a pair of laterals. The procambial strand of the second and succeeding leaves dies out, proceeding downwards. Consequently the cotyledon strand fuses only with traces from the first leaf. A little below the plumular bud, it approaches and immediately incorporates half of each lateral strand; at the same time, one sheath surrounds the strands from the first leaf and the cotyledon strand. Lower, the mid-rib divides, the halves lying on the arms of a right angle, about the "unfused" residue of the laterals. Further/

Further rearrangement by rotation gives a stele showing dipolarity, one pole contributed solely by the first leaf, the other by the leaf and cotyledon. Below the hypocotyl which is 1.5 mm. in length the stele is diarch.

Primary root.- is remarkable for the exceptionally strong nature of the endodermis. Not only is the latter made of large, greatly thickened cells, but at intervals it appears to be composed of a double layer. Further, the pericycle which is one layer in depth, has also very large cells. The cortex is wide and is doubtless responsible for considerable water storage. Raphides were observed in the outer cortical layers. They also occur profusely in the hypodermal layers and the mesophyll of the leaves. Glandular hairs were observed not only on the margin of the first leaf, but also on that of the cotyledon.

DYCKIA REMOTIFOLIA

The nature of the seed, embryo, germination and development was as for *D. floribunda*. The following record was kept of the progress made:-

4th/

- 4th March, 1929 - germinated
- 29th June - three foliage leaves expanded;
one adventitious root
- 22nd July - had three foliage leaves and
three adventitious roots, 10 mm.
long, in addition to the primary
root
- 24th August - 4-5 leaves. Height of plant,
12 mm. above soil, with three
adventitious roots (or less).
- 12th October - Five leaves; maximum height of
aerial portion 13 mm.
- 25th Jan. 1930 - Six fully grown leaves, bluish
in colour. Slow development
is clearly indicated.

Anatomy - does not differ essentially from *D. floribunda*. The single cotyledon strand remains independent for some length after the plumular traces have been resolved into a stele. Triarchy is indicated in the hypocotyl but the radicle is diarch. Again, there is a remarkable endodermal and pericyclic development, the pericycle almost constituting a second endodermis.

PUYA CAERULEA

Four seedlings examined.

Seed, Embryo and Germination as for Dyckia.

Seedling - characterised by its delicacy and transparency; the vascular tissue can be seen outlined if the seedling is examined with a lens. In structure it is simple consisting, like Dyckia, of -

Cotyledon

- (i) tip, fills most of seed, endosperm being scanty from the first,
- (ii) fairly wide lamina, photosynthetic, traversed by a single, rib-like cotyledon strand, terminating in
- (iii) short basal sheath, surrounding

Plumular Bud which is poorly differentiated.

First foliage leaf - is provided with a mid-rib and two laterals but development of this and later leaves is slow in the extreme.

Hypocotyl. At this stage when growth has proceeded for a few days only, the greater length of the seedling consists of hypocotyl which is a slender cylindrical organ. The hypocotyl persists at least for one year.

Primary/

Primary root - short and thin (less than 1 mm. long in day-old plant); persistent.

Anatomy. The "lamina" of the cotyledon shows a striking differentiation of tissue into a chlorophyllous layer in centre, (in which is embedded the solitary vascular strand) and water storage tissue. For the latter purpose the upper epidermis of very large cells, squarish in transverse section, has been utilised. The lower epidermis is composed of smaller cells. Simple glandular hairs cover most of the epidermis.

Transition. The traces of plumule and first foliage leaf reduce to two strands at the level where the cotyledon strand passes into the hypocotyl. The cotyledon strand unites with one of the pair. Hence a diarch arrangement prevails and half the root stele is derived from the plumule. The endodermis, as in *Dyckia*, is exceedingly strong.

First leaf. The three vascular strands lie in the chlorophyllous layer. The upper epidermis is specialised as a water storage layer, as in the cotyledon. Spines occur on the margin of the leaf.

PUYA COARCTATA

This species repeats in its seedling structure those features characterising *P. caerulea*.

The plumular stele is enclosed in a stout endodermis even before the cotyledon strand joins it. The cotyledon strand is itself efficiently ensheathed. The primary root is, unlike *P. caerulea*, triarch but the stele, in its sheath, is similar to *P. caerulea*.

AMARYLLIDACEAEAGAVE HETEROCANTHA

Germination and development of the seedling was observed until the second foliage leaf was produced. The stout green cotyledon bore the remains of the black testa of the seed for several weeks and continued to increase in length and girth, being 30 mm. long and 4 mm. in diameter when four weeks old. The seedling went through the same stages as LUBBOCK describes for *A. Wislizeni*. Thus the strong primary root persisted and elongated at the same rate as the cotyledon, which was cylindrical and succulent/

succulent and through which the first leaf emerged by a slit at the base. A cauline root was soon produced in the same vertical line as the plumular bud and the first leaf had a toothed margin. There was a marked development of hypocotyl (4 mm. long in oldest seedling) contrary to LUBBOCK'S observations for *A. Wislizeni*.

Anatomy. Throughout most of the length of the ^{cotyledon?} hypocotyl there were four vascular strands, equidistant from one another. Two strands are more strongly developed than the others, which are evidently subsidiary. Towards the tip these converged in pairs; the diameter of the cotyledon increased towards the sheath, the strands ramified giving four main and three subsidiary strands. The ground tissue is water-storing and the epidermis consisted of papillose cells, with a layer of wax on the outer wall. The hypocotylar stele consisted of a ring of xylem, outside of which were arranged four phloem patches. The primary root is four-arch.

SARGANT has described the transition phenomenon for *A. spicata* and *A. Rovelliana* which are also characterised by two main and two lateral strands in the hypocotyl and four-arch root. There is/

is a comparatively long hypocotyl traversed by three or four traces from plumule and cotyledon, possessing stem structure. Agave, according to SARGANT "is designed on a Liliaceous model". As far as the vascular anatomy of the cotyledon is concerned, it resembles the majority of the Amaryllidaceae examined in the present study.

3.

DISCUSSION.

DISCUSSION

The succulents examined have the following features in common:-

- (a) Type of germination and subsequent development.
- (b) Succulence.
- (c) Poor differentiation of plumule and consequent slow production of foliage leaves. The latter is possible on account of the assimilatory function of the cotyledon.
- (d) Simplicity in shape and anatomy of the cotyledon.

The number of vascular strands in the cotyledon depends on the family relationships however.

Thus the Bromeliaceae considered have the single cotyledon strand characteristic of all those members of the family studied. Here there is doubtless a case analogous to that of the aquatics, where apparent simplicity is more than probably a result of extreme reduction. The Aloineae, on the other hand, have retained the cotyledonary anatomy which is typical for the majority of Liliaceous seedlings, namely a pair of strands pursuing an almost parallel course. Agave, again, differs in no essential detail of its cotyledonary anatomy from other Amaryllidaceae of the most common/

common type.

- (e) Nature of the primary root, which is long lived and continues its growth steadily. It differs anatomically according to the family as one should expect from the variability of the number of cotyledon strands. Thus the Bromeliaceae have the simplest diarch stele, Agave a stele dependent for its symmetry on the four strands of the cotyledon. Aloe presents unusual features in the root. Apart from differences in the girth of the organ itself, certain species show specialisation of endodermal or hypodermal layers. The stele has not a constant number of xylem rays. The number extends from two to seven and varies even in the species where there are five or more, although species with diarch and tetrarch roots do not show this tendency. The aberrant types in Aloe may be an indication of the arborescent habit which does not make itself felt in the aerial organs of the seedling.
- (f) A habit which might almost be termed rosette, produced by simple radical sessile leaves, tapering towards the tip but with wide sheathing bases, which arise in very close succession on an axis devoid of internodes - for the upper surface of the/

the leaf sheath lies adjacent to the lower surface of that immediately above it. The result is a superficial resemblance in all these seedlings, but, as has been seen, this similarity in gross morphology does not extend to the detailed internal anatomy. It might be said that the habitat had induced a standardisation of form although it had not been necessary for modification in the vascular system to take place. Accordingly, the group as a whole lacks the unity observed in the aquatics, which are subject to an environment even farther removed from that of the normal geophyte, and one that is more uniform in its effects.

- (g) In conclusion it is interesting to note that KLEBS observed in succulents some of the adjustments to surrounding conditions, mentioned above; for example the persistent primary root.

B. E P I P H Y T E SBILLBERGIA

Seed was obtained from Marburg of *B. zebrina* and *B. Breauteana*. Four seedlings of each were examined.

BILLBERGIA ZEBRINA

Seed - roughly pyramidal in shape; about 4 mm. in length covered by a dark brown testa, strongly tanninised. The testa consists of two layers with the inner walls of the principal layer showing a remarkable development of thickening. The copious endosperm is starchy with the outermost layer composed of aleurone as in Grasses. The embryo is small, straight and cylindrical.

Germination. No definite mechanism is apparent for the rupture of the seed coat. The stout blunt radicle breaks through the testa at the apex of the seed, a ragged fringe of six-eight teeth being formed by the torn edge of the covering. This is accounted for by the nature of the thickening of the cell walls. The radicle itself is short, with a ring of root hairs at its upper extremity; its tip is merely a rounded knob with a massive root cap. In an eight days old seedling it is 8 mm. long, while the aerial portion of the seedling is only half this length (Fig. 22).

The/

The latter consists of cotyledon sheath and short ligule which is pierced by the first foliage leaf. The seed remains below the soil.

Cotyledon consists of:-

- (a) Suctorial tip - almost non-existent. In a seed $3\frac{1}{2}$ mm. long the tip is less than 0.5 mm. and, being blunt acts as a stopper to the seed. The connecting stalk region leading to the sheath is completely absent.
- (b) Sheathing base, tapering downwards to the primary root, and 1-1.5 mm. in length. It is partly covered by soil.
- (c) Ligule, the most noticeable part of the cotyledon in the growing plant. It is 1-2 mm. long and completely ensheaths the first leaf which breaks through by a circular opening at the apex.

Plumule. From the first is well developed occupying the bulk of the seedling.

First Leaf. Same shape as succeeding foliage leaves but never attains the size of the second leaf which in its turn is smaller than the third, and so on. It is simple anatomically and is traversed by a mid-rib and two lateral strands. Its maximum breadth and length are equal. The leaf is pointed. No unusual/

unusual feature calls for comment. The rosette habit which is adopted by the adult plant is indicated by the time that four or five leaves are expanded (Fig. 22).

Anatomy of young seedlings.

Two-days-old seedling.

The widest diameter of the plant is at the level of the plumular bud. The single cotyledonary strand proceeding downwards from the suctorial tip is diverted from its central position by the large mass of plumule and first leaves. Below the level of the plumule, the cotyledon strand moves inwards and is joined immediately by plumular traces. A stele, embodying three main xylem masses results. A scattered arrangement persists to the transition which occurs at a region corresponding to the upper limit of the root hairs externally. The root stele is triarch.

Six-days-old seedling.

Longitudinal sectioning confirmed the anatomy revealed by transverse sections of a similar seedling (Fig. 22). Owing to the development of cotyledon sheath and ligule it is necessary for the strand to pursue an oblique course upwards. It enters the plumular axis immediately below the base/

base of the ligule and continues an almost vertical course in the direction of the plumular bud. It gradually fuses with traces proceeding downwards from the latter, and at a point just below the meristematic mass. The axillary stele continuing downwards is very strong. Seven xylem groups are represented: when a level is reached corresponding to that of the soil, the xylem is consolidated into four, then two crescents. Further rearrangement gives a triarch plan, the xylem placed in a ring broken by three phloem patches.

A massive root cap protects the growing point in the young seedling.

Billbergia Breautiana

This species differed in no essential from *B. zebrina*. No description is therefore necessary.

MULLER figures six stages in the germination of *B. zebrina*. The stage where only a ring of root hairs occurs is not commented upon, in the text, or emphasised in the sketches.

Bromeliad 291.28.

Seedlings of this plant showed obvious affinities with/

with *Billbergia* in the type of seed, endosperm, testa and germination, nature of the cotyledon, radicle etc. The seed was obtained from British Honduras and up to the present has not been named.

The seed remains attached to the cotyledon for several weeks. Absorption of endosperm is slow, the suctorial tip being small. There is one strand in the cotyledon. The primary root persists and sends out lateral roots. The plant tends later to have a straggling habit, with hypocotyl and part of the first node lying horizontal in the soil. Accordingly the root system is reinforced by a few adventitious roots. The venation of the first leaf is similar to that of *Billbergia*. It is provided with marginal ocelli and glandular hairs and is delicate in texture.

Anatomy.

The stele of the strand running centrally through the first node consists of two well developed strands with the protoxylem patches almost touching, after the fashion of a double bundle: they are enclosed in a very well developed sheath.

The hypocotylar stele is characterised by a powerful sheath, consisting of a double layer of large strongly thickened cells. There are five patches of xylem (a little phloem being associated with /

with each) separated by rays of a single layer of parenchyma.

The root is 3-arch in a young seedling, 5-arch in an older one. The endodermis is remarkably strong.

A transverse section through the testa shows that it is composed mainly of a thick layer, reddish-brown in colour. This layer consists of two rows of cells with strong walls and completely filled with tannin. The outermost layer of the testa is made up of small rectangular cells, with thickish walls yellow in colour but having no cell contents.

AECHMEA GLOMERATA

The emergence of the radicle, its knob-like appearance and circle of root hairs in the first week are as has been described for *Billbergia*. SZIDAT (1918) who gives an account of the germination of *A. tinctoria* (Fig. 25) adds the information that the mechanical strength of the radicle is not entirely responsible for the rupture of the testa which is thickened like that of *Billbergia*. A chemical secretion produced by the radicle partially dissolves the cells of the testa in the neighbourhood of the growing point. The tip of the root becomes strongly coloured by the liberation of fluid from the tannin-ised seed/

seed coat. SZIDAT also notes the presence of a root cap and hypocotyl as well as the green cotyledonary sheath, which is pierced by the first leaf on the ninth day. He considers the germination exceptional in the root hair arrangement but connects the latter with the epiphytic habit as being advantageous in securing the plant's position on branches of trees. The poor development of the radicle, early appearance of adventitious roots, long functional of the suctorial tip of the cotyledon and adequate food reserve in the seed would then have to be considered from the same point of view.

Personal observations on the germination of *A. glomerata* confirm these notes. The pronounced ligular development, seen in *Billbergia*, is absent, though the slight arching upwards of the margins of the cotyledon sheath affords some protection to the plumule.

Anatomy of seedling five days old.

(a) Cotyledon. A single collateral strand extends from the tip, which is a well developed blunt organ, to the sheath. The base of the cotyledon is immediately below the plumular bud. Transverse sections show that, on the side remote from the seed, the sheath is slit, almost to the base, although/

although the overlapping of the margins minimise the exposure of the young leaves. The ground tissue of the cotyledon is composed of parenchyma. The stomata are sunk.

- (b) First and Second Leaves - have a mid-rib and a pair of lateral strands.
- (c) Hypocotyl. This is lengthy. It is traversed by a central collateral strand, with xylem and phloem strongly developed, an equal quantity of each being present. The remarkable endodermal sheath already referred to, in other genera of Bromeliaceae, is here present.
- (d) Radicle. The stele, in the piliferous region, is triarch. Its diameter is exceedingly small (Fig. 23).

In seedlings a fortnight old, there was a tendency for the seed to be lifted above the surface, possibly the result of the continued growth of the hypocotyl.

SURVEY OF THE LITERATURE ON
BROMELIACEOUS SEEDLINGS

Publications relating to the germination of epiphytes are few; doubtless owing to the difficulties involved in providing suitable conditions for the initial and therefore most critical stages of development.

KLEBS includes *Acanthostachys strobilaceae* in his Type I with an observation on the thick covering of long root hairs on the radicle.

The first suggestion that the seedlings of epiphytes would repay investigation was made by SCHIMPER, (108) who remarks that whereas reproductive organs and processes were not influenced by the plant's peculiar mode of life, germination might be exceptional, a hint which bore fruit in the work of F. MÜLLER (90) who made careful observations on seeds and seedlings mostly of the sub family *Tillandsiae* in 1895. His results will be considered in a general survey of the group. Nine years later BILLINGS (11) described a rarity, namely the germination of *Tillandsia usneoides* which usually propagates itself vegetatively. Unfortunately, he ignored the findings of MÜLLER on the genus. In 1922 SZIDAT (118) published an interesting review of the seedlings of Bromeliaceae/

Bromeliaceae and their adaptations to an epiphytic life. His study in some instances included the seedling, a description of germination being given for each grouping made. It is somewhat surprising and very regrettable that in no case did these workers extend their investigation to the internal structure of the embryo and seedling. BILLINGS mentions the number of strands in the first leaf of *T. usneoides*, a comparatively unimportant detail.

THOMAS and HOLMES (124) recently made a thorough research on the germination, seedling and young plant of *Ananas sativis*. A complete account of the anatomy is here available.

Before noting the peculiarities possessed by the seedlings, it may be profitable to consider their relationships. In addition to the accepted classification of Bromeliaceae, based on floral characters, the *Pflanzenreich* mentions groupings that have been based on vegetative characters and mode of life of the plant, e.g. terrestrial forms as opposed to facultative and obligate epiphytes.

TIETZE (125) has made three classes, taking into account the nature of the appendages of the leaf epidermis (stellate hairs etc.) and mode of nutrition.

(a) Terrestrial forms of low habit, having no special mechanism for conserving or obtaining water other than an efficient root system, e.g. *Puya* and *Dyckia*. /

Dyckia.

- (b) Terrestrial forms, e.g. Ananas and some Pitcairnia where highly specialised scales are provided for water absorption.
- (c) Epiphytes of low development with great leaves in a rosette and scales on the epidermis, the root system being weak.

KEILINE (79) making the habit of the plant and its leaf structure his bases, also obtained three groups.

- (a) Terrestrial.
- (b) Terrestrial but often epiphytic.
- (c) Purely epiphytic.

SZIDAT'S classification based entirely on the seed structure is most satisfactory. He describes the distribution of the family which is confined to tropical and sub-tropical America. Many genera are plants of the tropical rain forests: the necessity for marked adaptation to such a habitat is obvious. SZIDAT claims that the seed is absolutely diagnostic. His classification is as follows.

- I. Bromeliaceae - Testa without appendages. Seed pear shaped; embryo small; endosperm copious. Facultative Epiphytes.

II./

- II. Pitcairnieae - (a) Pitcairnia Type.)
Torpedo shaped)
seed.)
(b) Puya Type.) Terrestrial
Flattened seed,) wind
asymmetrical)
wing.) dispersed.
- III. Tillandsieae - Outer layer of testa hairy.
Obligate Epiphytes.

GERMINATION OF TYPES REPRESENTATIVE OF
SZIDAT'S GROUPS

II Terrestrial - Pitcairnieae

SZIDAT describes it for *Pitcairnia xanthocalyx* (Fig. 25).

I have followed the germination for this species and for *P. Andreana*. The terrestrial mode of life, according to SZIDAT, is indicated in the seeds of the genus by their specialisation for wind dispersal, being exceedingly light in weight with a membranous testa.

The germination is essentially the same as for *Dyckia* and *Puya*. * A ring of root hairs occurs at the upper limit of the radicle. There is a lengthy hypocotyl and a rather delicate cotyledonary blade with its tip imbedded in endosperm. From SZIDAT'S account it would appear that the seed is never lifted above ground/

ground by the erection of the cotyledon, hence the arched appearance of the young seedling in his drawings (Fig. 25). Actually the seed is lifted above the soil, not through the cotyledon blade becoming vertical, but by the rather rapid elongation of the hypocotyl before the first leaf develops. The testa drops off the tip of the cotyledon at an early stage (25). The scanty amount of endosperm is possibly correlated with the habit. Glandular hairs occur on the margin of the cotyledon.

Anatomy.

One is struck by the small delicate nature of the seedling and by the great simplicity in internal structure which is almost identical with that of *Puya* and *Dyckia* but on a much reduced scale. The seedlings examined were a few days old.

(a) Cotyledon. A single collateral strand acts as a mid-rib. The tissues are in no way remarkable. Four chlorenchymatous layers lie between the upper and lower epidermis which consist of small regular cells. (Fig. X). The plumule, at the stage of development sectioned, made no contribution to the root stele.

(b) Hypocotyl. A cylindrical structure with a central collateral strand enclosed in a sheath of/

of seven or eight very large cells, without marked thickening.

- (c) Primary Root. The stele is so small and simple that it can be regarded as monarch; three or four xylem elements are associated with a little phloem and confined by a strong endodermis.

(b) Dyckia and Puya Type

Has already been described. The most obvious difference from Pitcairnia is in the straightening of the cotyledon lamina and consequent lifting of the seed above ground from the first.

EPIPHYTIC TYPES

I. Bromeliaceae

The germination of Billbergia and Aechmea have already been discussed

Acanthostachys strobilaceae

KLEBS classes it with Type I, that is with seedlings having vigorous, persistent primary root and cotyledon one end of which remains in the seed while the other/

other forms a comparatively short sheath. He comments on the exceptionally thick covering of long root hairs (Fig. 25). A point of interest is that SZIDAT maintains that *Acanthostachys* diverges from the germination of *Aechmea* in having a club-shaped sucker, derived not from the tip but from the back of the cotyledon. This impression has been derived, apparently, from a consideration of the upper sheath round the plumular bud which now takes the pronounced hooded form which ARBER designates a ligule. The cotyledon of *Acanthostachys* seems to me to be exactly similar to that of *Billbergia* but with the "ligular" development more pronounced. *Aechmea* would then be regarded as providing a transitional type of cotyledon.

Ananas sativis

As has been mentioned, a very thorough investigation on the early life and structure of this plant was made by THOMAS and HOLMES, last year.

The seed is somewhat longer than for *Billbergia* but has the same type of leathery ridged testa, three layers thick. There are hairs in tufts on the ridges. An outer aleurone layer (cf. *Billbergia*) and a main mass of starch-containing cells comprise the endosperm. The food reserve is protein, starch and oil.

Germination/

Germination is of the normal hypogeal type (Fig. 26). Emergence of the radicle is passive, due to elongation of the cotyledon by expansion of its cells. A condensed habit is produced in the seedling by the rapid appearance of green leaves on an extremely short stem with practically no internodes. The primary root does not function long. It withers away, being replaced by adventitious roots which were developed along with the first leaves. Seven stages of germination are given. Development seems to run the same course as in *Billbergia*. After three weeks the cotyledon is a cylindrical plug hollowed to form a conical chamber in which the plumule develops with the wall thin on one side for its emergence. The radicle has been pushed out a little and a short cotyledon sheath produced in a month-old plant. The independent adult form is established after three months when the endosperm is finished and the primary root shed. Water storage is provided for by the hypoderm on the upper surface of the plumular leaves which have an elaborate coating of peltate hairs on both surfaces. The leaf strands are sclerenchymatous.

The anatomy of the young seedling is simple and ontogenetic development seems to be slow for at three weeks no vascular structure in the plumular position and/

and very little from the cotyledon is discernible.

A single collateral strand with phloem and xylem somewhat separated (Fig. 26) runs through the entire length of the cotyledon. One strand, less differentiated, comes from the first plumular leaf to contribute with the cotyledon strand, to the hypocotylar stele which is made up of a central xylem mass with two poles flanked by two phloem groups from cotyledon and plumule respectively. The early root, therefore, appears to be diarch. Later it shows three-four phloem and an equal number of xylem groups.

In adventitious roots the number of xylem poles is correlated with the diameter. A sclerotic middle cortex, a sclerised pith and a much thickened endodermis occur in many, although in short roots of large diameter these may be missing. Epicotylar and hypocotylar axes are short. A distinct stelar structure consisting of a pericycle of several cell layers is found at the level of insertion of the second leaf.

III. OBLIGATE EPIPHYTES - TILLANDSIEAE

The seed is long, thin and spindle-shaped (-), the embryo occupies more than one-third of the seed and the testa is the most specialised in the entire family, its/

its outermost layer having developed long silky multicellular hairs. SZIDAT divides the sub family into two groups:-

(a) that including Tillandsia, Vriesea, Guzmania and Sodirola;

(b) Catopsis.

(a). (i) VRIESEA TYPE

Vriesea vitellina.

MÜLLER (90) observed the germination of V. vitellina. The embryo is large, cylindrical and symmetrical, with feeble development of the plumule and little differentiation in the remaining organs. The basal end of the testa holds the radicle cap-fashion. On germination this cap-like cover is separated from the rest of the testa by a band, originally white, but turning green gradually. The band is the sheathing base of the cotyledon through the side of which the first leaf appears. No primary root develops. The "root cap" from the testa is so loosely placed on the radicle end that it is easily knocked off. (Fig. 28).

(ii) Tillandsia Type

Tillandsia/

Tillandsia Gardneri.

In this extreme type the embryo is still larger and occupies half of the seed. MÜLLER discusses the germination for a few species, e.g. *T. Gardneri*, *T. triticea*. Three or four days after sowing the awakening to life of the embryo is seen by the swelling of the seed and an alteration in its colour to green. The seed coat, too narrow to accommodate the bulky structure within, becomes loosened, but does not crack. In contradistinction to *Vriesea*, connection is not severed between the basal end and the bulk of the testa. The testa is intact until it is thrown off by the development of the first foliage leaf. It is interesting to note that the first leaf appears through the seed coat already equipped with a little lodicule, such as appears on the adult leaf.

Tillandsia usneoides.

BILLINGS describes the germination as normal; it occurred in the capsule following immediately on its dehiscence. There is complete absence of roots in the seedling and adult plant; no mention is made of a cap-like protection for the basal end of the embryo as in the *Tillandsias* studied by MÜLLER. The sheath of the cotyledon appears double due to the bifurcation/

bifurcation of a single organ. It arises on a single organ which is cotyledonary in nature and is possibly for the better protection of the stem apex. The leaf first attains considerable size before stem differentiation begins although in the adult plant the leaf is still small when the stem apex becomes distinguishable at its base. There are three vascular strands in the first leaf each with a sclerenchymatous sheath, lying in a ground mass of spongy parenchyma with small intercellular spaces. Water storage cells are placed between chloroplastic cells.

(b) CATOPSIS TYPE

The remarkable tuft of long silky hairs placed at one end of the seed is a diagnostic feature. Germination (Fig. 28) does not differ essentially from that of *Vriesea*. The cap from the testa covers the radicle end and the cotyledon is markedly swollen. Here as in other *Tillandsiae*, the radicle does not develop. The delicate hairs on the testa are hooked, a feature related to the habit of the plant. It grows exclusively on the branches of trees of the primaeval forest - the rough twigs afford an anchorage for the sharp hooks of the hairs.

S U M M A R Y

- (a) In this highly specialised family of strictly limited distribution, all types of germination are represented. Epigeal germination is characteristic for *Puya* and *Dyckia* in the *Pitcairnieae*, but the cotyledon of *Pitcairnia* itself in the early stages does not lift the seed above the ground although the cotyledon, as in *Puya*, is a leaf-like photosynthetic organ becoming more or less horizontally placed; *Pitcairnia* is, therefore, a transitional type. In the *Bromelieae* germination is hypogeal, but whereas the cotyledon sheath of *Aechmea* consists merely of the base of the seed leaf, there is in *Billbergia* a distinct "ligule" for protection of the first leaf, a feature common to *Acanthostachys*. As one should expect, abnormalities occur in the germination of the *Tillandsieae*. The greater part of the seed is carried up on the enlarging cotyledon in *Catopsis*, *Vriesea* and the *Tillandsias* so the term epigeal might be applied to it. There is therefore no exact relation between the epiphytic habit and type of germination (epigeal or hypogeal).

(b)/

(b) There exists a uniformity in the nature of the endosperm (starch, with an outer aleurone layer) but not in the proportion present in the seed. Although the testa gives a bulky appearance, the seeds of the Pitcairnieae are the smallest (one-third - one mm. long) and the embryo occupies more than half the seed. The Tillandsieae have long but narrow seeds (7 mm. for Vriesea, apart from hairs) and in addition the space taken up by the embryo is considerable (one-third to one-half the seed). The seeds of the Bromeliaceae are much larger and heavier, however, e.g. Aechmea is 1-2 mm. long, Acanthostachys $2\frac{1}{2}$ -3 mm., Billbergia 3-4 mm., Bromelia 5 mm.; and, since in all the embryo is small, there is a preponderance of endosperm. Size of embryo, then, is not directly related to the epiphytic life, for large embryos are found in the Pitcairnieae. But the weight of endosperm seems to influence the type of germination, as far as this family is concerned. It has been suggested that the large food reserve in the seed of the Bromeliaceae is a factor favouring their habit (118).

(c) With regard to the development of primary root, this/

this is variable in the extreme. Thus, at one end of the scale, are found terrestrial types with persistent radicle endowed with vigour from the first, on account of its importance as the sole source of water. At the other are the obligate epiphytes which never possess a primary root, and intermediate are the facultative epiphytes, including rock and sand plants, the radicle of which is at first short, although it elongates later, and persists for three or four months.

- (d) The more the primary root is restricted in its development, the better is the root tip protected. So, in the terrestrial forms, the tip is protected in the normal fashion; in *Billbergia* and *Aechmea* there is a remarkably strong root cap. A still more effective device is given by the basal end of the testa in *Tillandsieae*.
- (e) Root hair production varies in its scope. The ring of root hairs in the *Bromelieae* may compensate for the shortness of the radicle. More possibly it acts as an anchorage (cf. *Aquatics*) for the seeds are not provided with long, entangling hairs, hooks or gummy substance for their attachment/

attachment to a spot suitable for germination (118). *Acanthostachys* is exceptional in having a mass of long root-hairs covering the radicle. In this it resembles the *Pitcairnieae*, in which the need for deep and efficient rooting is obvious.

- (f) Plumular development also varies; on the whole it tends to be more backward than in seedlings of geophytes. The lack of differentiation in the embryo and seedlings has been mentioned in the literature for *Tillandsia usneoides*, *Ananas*, and *Vriesea*. The seedling of *Dyckia*, *Pitcairnia* and *Puya* may be three or four weeks old before the first leaf is discernible. Here there is no necessity for an early photosynthetic foliage leaf. Yet in *Tillandsia*, with no leaf-like cotyledonary blade, the same period elapses. The first leaf of *Billbergia* and *Aechmea* makes its appearance a few days after germination, but *Ananas* of the same group is exceptionally slow in its production of leaves.
- (g) The shape and size of the suctorial tip of the cotyledon differs also, in the three classes. It remains short and thick set in the *Pitcairnieae* but in the *Bromelieae* is a long-functioning organ which is short, blunt and stopper-like. No distinct/

distinct suctorial organ at all is differentiated in the Tillandsieae.

- (h) As is only natural, a well marked hypocotyl is found in none but terrestrial forms.
- (i) The anatomical simplicity of Bromeliaceous seedlings and the constancy of certain features, e.g. nature of cotyledon strand, endodermis of root, etc., finds an explanation in the idea of extreme reduction as a result of habitat, the final stage being seen in *Tillandsia usneoides* where degeneration of the vascular strands is to be seen.
- (j) The striking adaptation of the seed coat to bring about dissemination, and, in the case of epiphytes, anchorage of the seed has been fully discussed by SZIDAT.
- (k) Odd points of general interest, revealed by a study of seedlings of Bromeliaceae are:- the double sheath of the cotyledon of *Tillandsia usneoides*; the liberation of an enzyme to assist the radicle to rupture the seed coat of *Aechmea*; the occurrence of glandular hairs even on the cotyledon of several genera; the very slow ontogenetic development of *Ananas sativis*, and the/

the somewhat unusual course pursued by the vascular strand of the cotyledon of *Billbergia* to ensure adequate food supply to the vigorously growing plumule. Whether the cotyledonary strand of *Aechmea* behaves in a similar fashion has not yet been determined.

PLANTS WITH PERENNATING ORGANSA. BULBOUS

The two families, Liliaceae and Amaryllidaceae, in which bulb formation is prevalent, provided material for examination.

LILIACEAETribe - AsphodeleaeBOWIEA VOLUBILIS

The plant belongs to the same group as Anemarrhena, on the seedling of which SARGANT based her theory of the Double Bundle (102, 103). It is described by LUBBOCK (86) and ARBER refers to its floral axis, its heterophily, and the ring arrangement of stem vascular strands as in a Dicotyledon. No anatomy is given, however. Ten seedlings were sectioned.

Germination. Type 5 KLEBS. As this type of germination is constant for all the bulbous types which I have examined, it will be described only for Bowiea.

The youngest seedling shows the radicle protruding 1 mm. from a rupture in the seed which lies horizontally in the soil. Curvature of the radicle downwards and elongation of the cotyledon axis results in anchorage of the root and raising of the seed/

seed on a vertical cotyledon (Fig. 31). At this stage the plumule is poorly differentiated; it is completely sunk in tissue, being placed almost centrally at the base of the cotyledon, lateral to the cotyledon strands and at soil level. Its development is slow. From the first, provision is made for the emergence of the first leaf by a slit in the base of the cotyledon.

The cotyledon is simple in structure, showing little differentiation of tissues. As it emerges from the seed, it assumes an assimilatory function and, for a year, is the only photosynthetic organ. During the first month, it elongates rapidly. It is cylindrical, tapering from the base upwards, with the seed at its tip, which later withers and casts off the empty testa.

Anatomy

(a) Cotyledon. Two parallel strands run from the tip to the base. They tend to converge to a central position at the level of the plumular bud but do not fuse until they are below the plumule, at which point a crescent of xylem forms. Complete fusion of cotyledon and plumular axis having occurred, the xylem becomes consolidated to a triangular plate which is surrounded by a ring of phloem. Owing to its slow development, the plumule/

plumule makes no real contribution to the root stele.

- (b) Radicle. An endodermis now surrounds the vascular tissue, which is typically triarch. One layer of pericycle is present but little or no parenchyma. The diameter of the stele is one-half the width of the cortex. At the level of the plumule a collar of tissue, three cells deep, surrounds the margin of the base of the cotyledon. It is piliferous and continuous with the root epidermis. The xylem breaks up into three small groups at the root tip.

The triarch root pole clearly consists, in older seedlings, of tissue two-thirds of which have been contributed by the cotyledon, the remainder coming from the plumule. In the youngest seedling however, an even higher proportion of root stele is cotyledonary in origin; in spite of this, triarchy characterises the early stages. (SARGANT'S observations on other members of the Tribe point to triarchy in the radicle as being derived from cotyledon and plumule, in the proportions shown by the older *Bowiea*).

At later stages the primary root becomes contractile, pulling the bulb, which forms, below soil to a depth of $1\frac{1}{2}$ -2 cm.

(c)/

- (c) First leaf - appears through the cotyledon slit, as a small lateral stump. When fully grown it resembles the cotyledon in being cylindrical, rather succulent and very lengthy. Originally it has five vascular strands, but later ten.

Development of Bulb

On 18th February, 1928, no trace of swelling at the base of the cotyledon had occurred, although many cotyledons were vertical and approximately 4 cm. high. They continued to elongate and seedlings collected on 17th March had cotyledons 6 cm. high; little in the nature of basal development had taken place but the first leaf had emerged about 1 mm. through the sheath. Seven weeks later a typical seedling showed the beginning of bulb formation. The swelling at the base of the cotyledon was 4 mm. in diameter extending through 6 mm. of the sheath in a cotyledon 8 cm. long. The primary root, now contractile, was reinforced by one cauline root.

When the plant becomes bulbous, the base of the cotyledon has to increase in width, to accommodate it. This increase takes place abruptly, within a few mm. Consequently, in a year-old specimen (Fig. 31) three additional strands run parallel to the original pair; these supplementary bundles and several ramifications come/

come off at right angles as the abrupt increase in girth occurs. They enter the axis and are superposed upon the plumular traces before the latter fuse with the cotyledonary strands. Thus, although older seedlings show the transition already described, there is the further complication of the subsidiary strands and their joining the traces from the five strands of the first leaf (Fig. 33).

Lateral roots, and cauline roots from the base of the bulb, are produced sparingly. After a year there may be only three or four roots but these are thick and strong. The central cortical zone and the hypodermal layer seem to function as a store for water in seedlings of this age (Fig. 32). The tissues are identical for primary and adventitious roots, save that the stele of the latter may be five- or six-arch.

During the winter period, the aerial portions of the plant died down. Observations were next recorded on 18th April, 1929, (Fig. 31). Dissection reveals a plumular bud at the apex of a short cone-shaped axis in which the characteristic curvature of leaf traces for Monocotyledons is easily traced (Fig. 32). The leaf nearest the bud is still inside the bulb and is surrounded by the bases of two aerial leaves, 17.5 and 10.5 cm. being their respective total/

total lengths. The latter are ensheathed at the base by a leaf base and the cotyledon base, both of which are fleshy.

The floral axis was produced at the beginning of June, 1929. It emerges, showing at once the climbing habit. Although there is no support, it twists spirally, and attains a height of 5 cm. in three days. It bears a terminal bud and two short branches laterally, each subtended by a scale. The stem is bright green to within 4 mm. of the base even where encased by the bulb, which is semi-transparent.

At this, the final stage examined, the maximum diameter of the bulb is 1.5 cm. It consists chiefly of three transparent bases of aerial leaves, mucilaginous within the epidermis, each entirely enfolds the leaf base underneath it. Below these is a thinner scale (apparently never possessing an aerial part) and still nearer the centre, the base of the current year's oldest green leaf, of which a considerable portion of "lamina" has died back. Its base is not sufficiently wide to encircle the slender scale leaf, the base of the second green leaf and the climbing axis within. Four or five minute, colourless scales are arranged in a whorl round the base of the latter. There are now five long, generally unbranched, contractile roots placed centrally at the base of the bulb.

Tribe/

Tribe Scilleae.ORNITHOGALUM SP.

The anatomy of the young seedling having been worked out by SARGANT (102), no description will be given here. CHOUARD'S sketch of the seedling of *O. pyrenaicum* is reproduced (Fig. /).

Description of 11-months-old seedling.

The only photosynthetic organs are the cotyledon and one or two leaves. The bulb is produced by the swollen bases of these.

Cotyledon - consists of a much swollen, water-storing sheathing base approximately 20 mm. long, 7 mm. in diameter, through which pass two main strands (the original strands) and two parallel subsidiary strands, joining the others at soil level. The aerial, green portion of the cotyledon is cylindrical, 50 mm. long, having two strands. It is heavily cutinised on the outer epidermal walls. The seed even at this stage adheres to the suctorial tip.

Plumule - occurs at the base of the cotyledon sheath, therefore some distance below the surface. It is slow in development.

First Leaf. Is the same length as the cotyledon and similar/

similar to it in appearance. In transverse section it is hexagonal. The outer epidermal walls are covered with thick cuticle, which projects at the corners. The epidermal cells are elongated radially. Immediately below is the palisade layer, one cell (frequently two short cells) deep. One main and two lateral strands (Fig. /) lie at the corners of a triangle, in a mass of parenchyma with small inter-cellular spaces.

Primary Root. Is persistent and at an early stage becomes contractile. It is reinforced by two cauline roots from the base of the cotyledon and lateral roots may be produced by these. The radicle was found to be triarch and tetrarch, while the adventitious roots were tetrarch and pentarch. The stele of all the roots is approximately one-ninth of the total diameter.

If the base of the swollen region of the seedling be sectioned, a region is found, extending through one-half mm. in which the primary and adventitious roots are imbedded in a parenchymatous ground mass; this may be the result of persistence and further development of the "collet", observed by SARGANT in the young seedling.

CHOUARD figures *O. flavum*, germinated from seed from the Botanic Garden at Geneva. The seedling is quite/

quite abnormal, not only in the type of germination, but also in its vegetative habit which is totally unlike the bulbous type described. If the plant is indeed that of the genus *Ornithogalum*, then it is aberrant not only with respect to the rest of the genus, but in relation to seedlings of all other bulbous forms examined. CHOUARD states that it presents in an exaggerated manner the same type of germination as *Merendera bulbocodium* (which will later be discussed), that it possesses a long ligule on the cotyledon, a well developed first leaf which is triangular in outline and a radicle pierced and later supplanted by a remarkable adventitious root. The latter becomes enormously swollen with food which would otherwise be available for the plumule. Even the nature of the perennating organ is therefore different for this seedling.

LACHENALIA SP.

Four seedlings were examined (Fig. 36).

Germination, Cotyledon - position and development of plumule as in *Ornithogalum*, but the cotyledon sheath elongates to pull the plumule deeper into the soil so that the seed is kept underground. The cylindrical first/

first leaf elongates rapidly.

Primary Root - persistent. Its length corresponds roughly to that of seedling above the surface. A ring of stout root hairs occur, at the upper limit. In a seedling a few days old, a cauline root arises directly in a line, vertically, with the plumule.

Anatomy. SARGANT (102) has described the transition for *L. Nelsonii*. Like the latter species, there is here a main double bundle in the cotyledon and, in addition, two lateral strands. The first leaf traces join those of the cotyledon just below the plumular bud. Unlike *L. Nelsonii* the radicle is triarch and not diarch.

Tribe Tulipeae.

LILIUM MONODELPHUM VAR. SZVITZIANUM

Three seedlings were examined.

Seed 5-7 mm. long; flattened. The seed coat is black and rather thin.

Germination. Type 5, but differs from the *Bowiea* germination in a further differentiation of the cotyledon (Fig. 37).

Cotyledon consists of:-

(a)/

- (a) a sheathing base swollen for food reserve: it is less swollen towards the margins and is an exceedingly effective sheath. It is folded round the plumule and first leaves so that it overlaps considerably. It narrows to
- (b) a stalk of equal length, and
- (c) an expanded lanceolate lamina, which develops as the suctorial tip is withdrawn from seed on the disappearance of the endosperm.

The stalk and lamina alone are above the surface and are photosynthetic.

Plumular bud. This is strong, but slow in development. It arises at the base of the cotyledon, below the surface. The internodes are practically absent.

First leaf - possesses three main strands.

Hypocotyl - is very short.

Primary Root - is persistent. It is strongly lignified, with a very stout endodermis and, by the time the first leaf is above the soil, is reinforced by adventitious roots.

Anatomy. A double bundle extends from the tip to the base of the cotyledon as was noted by SARGANT (103). The parenchymatous ground tissue is abnormally /

abnormally developed for storage purposes. The strand of the cotyledon passes swiftly but in two portions at slightly different levels, to fuse with the strands from the first and second leaf. The maximum diameter of the seedling is at the lower limit of the cotyledon. The beginning of the root cortex can be distinguished, embedded in the parenchyma of the cotyledon. The root stele is typically tetrarch; this is reduced to triarchy as the girth of the root decreases, and all traces of cotyledonary storage cells have disappeared. At a slightly lower level two protoxylem arms fuse and the root structure becomes diarch.

FRITILLARIA SP.

SARGANT gives the detailed anatomy for *F. imperialis* which follows the *Tulipa* type seen in *Lilium*. The two traces of the cotyledon are inserted on those of the ^{plumule} cotyledon at the first node where the transition begins, but tetrarchy or hexarchy may occur, which is explained by the persistence of the primary root.

In the species examined the tetrarch primary root in the young stage had an exodermis of very large cells. A year old seedling has no foliage leaf although a small outgrowth is appearing through the cotyledon sheath. The part of the cotyledon above/

above ground is cylindrical and still carries the seed at its tip. The base has become swollen and forms the small bulb, which is pulled deeper into the soil by the contractile radicle.

Sections through an old primary root show how efficiently the stele is constructed for its lengthy function. The endodermis has become so strongly thickened that only a very small lumen remains (Fig. 39). Of the original tetrarch symmetry no trace remains for the xylem is now a stout hollow cylinder. A ring of large, thin-walled cells separates the latter from the endodermis.

NOMOCHARIS PARDANTHINA

Seed, Germination and Description of Seedling as for *Lilium*.

The cotyledon in the young seedling is a delicate cylindrical organ. The primary root in the early stages is also very weak.

Anatomy.

A double bundle is found in the cotyledon. The primary root has a small stele which is diarch, four or five xylem elements being disposed in a strip across it.

A seedling six weeks old shows the first sign of bulb formation by the noticeable swelling of the base of the cotyledon. At this stage the cylindrical cotyledon has changed to a more flattened structure although not so pronouncedly as in *Lilium*.

LITERATURE ON THE SEEDLINGS OF
BULBOUS LILIACEAE.

SARGANT, whose theory of the origin of monocotyledons was founded on seedlings of Liliaceae, describes several seedlings of bulbous plants (—), viz. *Albuca*, *Allium*, *Chlorogalum*, *Eucomis*, *Erythronium*, *Bloomeria*, *Hyacinthus*, *Galtonia*, *Muscari*, *Milla*, *Scilla* in addition to those, e.g. *Fritillaria*, to which reference has been made. It is sufficient to note here that in all these genera the germination is KLEBS Type 5, that the cotyledon, except that of *Erythronium*, is supplied with two strands or their equivalent, and that the root poles number three or four, five being exceptional. ROBERTSON (100) in a paper dealing with the movement of bulbs in the soil (migration, and descent by contractile roots) and the formation of droppers, cites *Tulipa* and *Erythronium* as providing examples of the latter. *Tulipa* conforms to/

to the double-bundle type with diarch root; the dropper is cotyledonary in origin and therefore supplied by branching of the cotyledon strand. Her account of the origin of the dropper in *Erythronium* which is unusual in having three cotyledon strands, is less clear, but she explains the triarch root as a necessity, for the plant is dependent on it for a long period, while SARGANT gave, as the reason for the aberrant cotyledonary anatomy, the early transformation of the first leaf to a dropper. The most satisfactory account of the dropper of *Erythronium* is given by BLODGETT (12) who indicates clearly, however, that it is cotyledonary and not plumular in the first instance. His description is of *E. americanum* which has two vascular strands in the cotyledon which functions as the first and only foliage leaf of that year. He correlates the delayed germination with the large store of endosperm and the development of the primary root with the exhaustion of the reserve, while the short period of vegetative activity is an adjustment to short growing seasons.

CHOUARD (25) has recently published a very full description of the seed and seedlings of the tribe Scilleae. They present no feature which is exceptional. He divides them into two groups according to/

to the type of germination, whether hypogeal or epigeal (this will again be mentioned). In the Scilla type, the great mass of the embryo is cotyledon (Fig. 34). The seedling has a cylindrical, photosynthetic cotyledon with two vascular strands, though the number increases to four or six in the swollen base (cf. Bowia). The primary and sole root is tetrarch; it is contractile. The plumule is pulled deeper into the soil, is surrounded by three or four scales and, becoming tuberos, forms a little bulb. A comparison is made between the cotyledon and the first leaf. The Endymion type has a cotyledon always underground (Fig. 34), again with two vascular strands. The plumule is larger, (doubtless as a result of the subterranean cotyledon - L.B.). The cotyledon is compared with the scale leaf of an adult bulb (see Final Summary). A Key which takes into account divergences from the two main types, e.g. varying lengths of the sheath, rate of germination is given for the tribe. The third group in this classification is concerned with "the hypogeal cotyledon with a prolongation in the form of a ligule", the sole example being the rather questionable *Ornithogalum flavum*.

SCHLICKUM examined two bulbous types, for the purpose/

purpose of comparing first leaf and cotyledon.

Both (*Hyacinthus candidans* and *Allium fistulosum*) have KLEBS Type 5 of germination, and have cylindrical photosynthetic cotyledons with two strands in that of *Hyacinthus* and one (double bundle) in that of *Allium*.

KLEBS mentions the production of a bulb as characteristic of seedlings of *Lilium*, *Gagea* and the genus *Allium*, and places several, e.g. *Fritillaria*, *Ornithogalum*, *Scilla*, in their group.

AMARYLLIDACEAE

The seedlings are of plants all belonging to the tribe *Amaryllidoideae*. Two groups can be made for the seeds of *Amaryllidaceae*. When they are numerous ^{small} they are flattened and winged, but, when few, they are large, green and irregular in shape many being bulbiform. This has been noted by RENDLE (95) who remarks that the type of germination for the family is the same as for *Liliaceae*. It will be seen that the bulbous types in their germination resemble those seedlings just described; they can be referred to a central type (KLEBS Type 5).

GROUP I. SEEDS NUMEROUS.

HIPPEASTRUM/

HIPPEASTRUM.

Three species were examined, viz. - *H. advenum*,
H. bicolor and a hybrid from two unknown species.

HIPPEASTRUM X.

Seed, for this and the other two species, was light in weight, flat, covered with a black papery testa. Length approximately 1 cm.

Germination. The cotyledon is thin, green and cylindrical. The sheath is the most conspicuous part. The radicle is at first short but in a few days it elongates rapidly, keeping pace in growth with the cotyledon; it is persistent, increases in girth in the upper part as it becomes a water storage organ and later is contractile. A slit is provided for the emergence of the plumule from the first, but the sheath elongates considerably before the first foliage leaf emerges, which it does in a week or so. There is a distinct swelling of the cotyledon sheath at an early stage (Fig. 40) giving a bulbous appearance to the very young plant.

Anatomy (Fig. 40).

Cotyledon. The ground parenchyma is water storing and mucilaginous. A pair of vascular strands proceed from/

from the tip to the base of the cotyledon, turn towards the centre abruptly and fuse with the plumular traces.

First Leaf - has a mid-rib and a pair of lateral strands.

Primary Root - triarch at the upper limit (two-thirds of the stele being derived from the strands of the cotyledon). It changes lower to diarchy and as it tapers to the tip, the xylem is reduced to a few elements. The cortex is enclosed by a double layer of large squarish cells of equal size which may be regarded as a multiple piliferous layer, or an outer piliferous layer and an exodermis, the existence of which is related to the succulence of the cortex.

HIPPEASTRUM ADVENUM - differed from *Hippeastrum X* in one respect, viz. that the sheath of the cotyledon in the former seedling showed no very perceptible swelling due to succulence.

HIPPEASTRUM BICOLOR. Germination and external morphology indistinguishable from those of the other species. Anatomically it showed differences in the structure of cotyledon and root. The cotyledon was supplied by three strands which might be regarded as a mid-rib and two lateral strands, the latter derived from the splitting of single strand for no apparent reason./

reason. The primary root is tetrarch and not triarch. (Transition in Fig. 40). First leaf as in Hippeastrum X.

ZEPHYRANTHES SP.

Germination and Seedling - as for Hippeastrum bicolor.

Anatomy - as for Hippeastrum advenum and Hippeastrum X, i.e. two parallel strands descend through the cotyledon strand, forming part of the triarch root stele. The first leaf is almost cylindrical; it has a mid-rib and a pair of lateral strands although the number of strands increases to five at the widest part of its sheath.

NARCISSUS EGLINTONI

Germination and Seedling - as above.

Anatomy. Like Agave, there are two strands in the suctorial tip and an extra pair of subsidiary strands in the sheath. The primary root is tetrarch. The piliferous layer is made up of very small cells; there is an exodermis of very large squarish cells. The first leaf has numerous strands, there being a prominent central bundle, surrounded by eight small peripheral/

peripheral strands.

PANCRATIUM

Three species were examined viz. *P. foetidum*, *P. maritimum* and *P. canariensis*; young stages of the latter were not obtained.

Pancratiium foetidum. Germination, morphology of seedling and anatomy of cotyledon similar to those of *Narcissus Eglintoni*. The root stele is tetrarch, with the xylem rays meeting in the centre instead of being peripheral as in *Narcissus*. The first leaf has a mid-rib and two lateral strands.

Pancratiium maritimum. There are two strands in the tip of the cotyledon and two in the sheath. But throughout most of the latter region one of the strands is composed of two distinct rays of xylem. The primary root is tetrarch, the four xylem groups being peripherally arranged in the stele. There is a mid-rib with a pair of lateral strands in the first leaf, the sheath of which has a further pair of lateral traces.

Pancratiium canariense. The seedling examined was three months old. Only a fragment of thin papery cotyledon/

cotyledon remained, wrapped round the swollen bases of the first two foliage leaves. Two cotyledon strands could be distinguished but it was impossible to determine whether subsidiary strands had been present. The first leaf had ten vascular strands in the sheath which was a hollow cylinder enclosing the base of the second leaf; the latter had five vascular strands. The base of the long bulb consists of a ground mass of storage tissue, welding together three roots, one the original tetrarch root of the young seedling, the other being polyarch (seven or eight xylem rays) (Fig. 41). The primary root has a remarkably strong endodermis which is fortified further by thickening of the innermost layer of the cortex.

GROUP II. Seeds few.

The seeds are among the largest encountered in this study, but although bulky, they are not necessarily heavy. Their true nature was the subject of a considerable amount of discussion extending over a long period. RENDLE (95) sums up the history of it and divides the bulbiform seeds into two groups, the first again being sub-divided -

A. i. that in which the bulbiform mass is derived from the outer integument, e.g. *Hymenocallis*;

- ii. the seeds of which are naked ovules, the endosperm providing the fleshy substance, e.g. *Crinum*.

B. in which a bulbil is formed to replace the seed before germination, e.g. *Calostemma*.

BRUNSVIGIA

Two species from South Africa, still unnamed, were examined.

BRUNSVIGIA K. 59 (from the Drakensberg)

Seed. A month after germination is somewhat shrivelled. It consists of a fleshy spherical mass of parenchyma approximately 12 mm. in diameter with an outer corky covering, four cells deep; there is no true testa.

Germination. The cotyledon is a bulky organ. There is a conspicuous sheath. In a few weeks the sheath may be 2.5 cm. in length and 0.5 cm. in diameter. The stalk connecting sheath and seed may itself be 1.5 cm. The first leaf breaks through the sheath where it bends towards the seed. Germination is clearly KLEBS Type V. but instead of the seed being lifted into the air by the straightening of the cotyledon/

cotyledon stalk, the plumule is carried downwards into the soil by an elongating sheath. The seed is eventually pushed above the surface. Owing to the weight and bulk of the seeds in this and other genera, the problem of mechanics in raising them must be serious.

The primary root is long, tapering and succulent. It is persistent.

Anatomy. This corresponds to the massive character of the seed and seedling.

Cotyledon. In the suctorial tip which occupies one-third or half of the seed and maybe 2 to 4 mm. in diameter, there are nine strands, each enclosed in a firm parenchymatous sheath. Ramifications are rare. Towards the extreme tip the strands fuse in pairs, which converge in the centre. There are nine strands in the cotyledon sheath which tends to be mucilaginous.

Radicle. There is a small-celled epidermis from which root hairs are noticeably absent, an exodermis of large cells, a wide water storing cortex and a strong stele with ten protoxylem groups and metaxylem scattered irregularly towards the centre. (Fig. 42).

First/

First and Second Leaf - have nine vascular strands arranged as four pairs of lateral traces, about a mid-rib.

BRUNSVIGIA K 64. - is similar in every respect to the species already described save that the root is hex-arch and that the cotyledon has six traces in the sheath, with the outermost pair ramifying at the base. The seedling at the same stage of growth, is smaller than *Brunsvigia* K. 59.

CLIVIA

Two species, *Clivia miniata* and an unnamed South African species (*Clivia* K. 101) were sectioned.

CLIVIA MINIATA.

Seed larger than for *Brunsvigia*. Hemispherical in shape, consisting of firm fleshy tissue protected by a thin brown covering which readily peels off. The seed becomes pale green at germination.

Germination. The massive blunt radicle grows vertically downwards; from the initial stage it is very thick and has a blunt conical tip. The plumular bud is seen in a few days as a lateral bud. From this period, the seed is raised upwards through the soil through the exertions of root and lower part of the cotyledon. The swelling of the plumular bud and its/

its emergence seem to crack the seed. The cotyledon differs from that of *Brunsvigia* -

- i. in having a shorter sheathing base (less than 5 mm.),
- ii. in lacking the lengthy stalk connecting the tip and sheath.

A further difference in the seedlings is that the first leaf produced by *Clivia* is a short clasping leaf. The true foliage leaf succeeds it, appearing one month after the commencement of germination.

Anatomy.

Cotyledon - has ten vascular strands throughout its length.

Primary root stele has approximately ten xylem rays. There is a wide cortex surrounded by a thin-walled exodermis and a multiple piliferous layer. Almost every cell of the latter shows a reticulate thickening of rods which are highly refractive (Fig. 44).

First Leaf - has nine parallel strands, although this number is increased to thirteen towards its base.

CLIVIA K 101.

The seedling is still massive although smaller than c./

C. miniata. The seed is the same size as that of *Brunsvigia*. It differs from *C. miniata* anatomically-

- i. the cotyledon has only six vascular strands;
- ii. the root is heptarch, but has the same type of cortex, exodermis and multiple piliferous layer.

CRINUM

Two seedlings of an unnamed *Crinum* (K 34) and the seed of *C. Macownii* were examined.

CRINUM MACOWNII

The truly remarkable seed of *Crinum* is that most discussed in the literature of the bulbiform seeds of the family. But, as in the case of other Amaryllidaceous seedlings of this group, no anatomical details are available. The seed of *C. Macownii* is soft and light, fig-shaped and approximately 6 cm. long. The spongy, pale green endospermic mass is surrounded by a network of strong tracheids and vessels, spirally thickened, which proceed from a stalk, doubtless the original funicle. They were recorded by BRAUN (17) as being in the fleshy mass, but by SALISBURY (95) as entering at the hilum and being distributed round the margin. The embryo is egg-shaped, well differentiated, (Fig. 46), and though it appears small when seen embedded in the fleshy/

fleshy mass, is actually of large dimensions being 3-6 mm. in length at maturity. The great bulk of it is cotyledon.

CRINUM SP. K 34.

Seed - large but has not the dimensions of *C. Macownii*.

It is on the average, 15 mm. long. Like other *Crinum* "seeds" it is covered by a thin corky layer.

Seedling. Germination is Type V. but the cotyledon is peculiar in the following respects:-

- i. There is a remarkable development of sheath, which soon becomes greatly swollen. The sheath may attain different lengths according to circumstances (95) e.g. *Crinum capense* when germinated on the edge of a board showed an exaggerated development of the sheath.

RENDLE () reproduces VAN HALL'S figure of this seedling (Fig. X).

- ii. The stalk region, in addition to its unusual thickness, twists in an irregular fashion. Its course is meandering and of considerable length, reminding one, on a smaller scale, of the germination of the double coconut.

FISCHER (43) referred to it as a "worm-like elongation". According to SALISBURY no law governs/

governs the point of emergence of the original process from the bulbiform seed, hence claims WORSELY (131), the need for such curvature.

But, even allowing for the difficulties of emerging from such a seed and finding a downward direction, it is not clear why so many twists are necessary.

iii. The suctorial tip is a blunt finger-like or club-shaped organ. The twisting of the stalk finds a repetition in the tip which may bend in the endosperm in any direction. This has been figured by at least two authors, viz. RENDLE who gives SALISBURY'S drawing () and ARBUR (p.17).

Anatomy.

Cotyledon - has six strong vascular strands in the tip and stalk. The number increases to ten in the swollen sheath.

First Leaf - has a mid-rib and two pairs of lateral strands.

Primary Root - is less well developed than one would expect. The seedling seems to be to a certain extent independent of the radicle. WORSELY observes that/

that for *C. Moorei* there may be no sign of root "until the seed is quite dead and the bulb is formed". It is then that, three months after germination, several roots are produced simultaneously. There is a prominent stele which is hexarch, and a multiple piliferous layer with reticulately thickened cells.

HAEMANTHUS SP. (K. 92)

Seed - pear-shaped; approximately 1 cm. in length.

Germination and type of seedling - as for *Clivia* (Fig. ~~X~~).

Anatomy. The cotyledon has six strands and is a succulent organ which is forced to widen to accommodate the swollen leaf bases of the plumule. There are eight strands in the first leaf. The short primary root is thick, succulent, and contractile from an early stage; the stele is tetrarch, the cortex wide and mucilaginous and there is a multiple piliferous layer, three cells deep (Fig.). The fact that the primary root remains relatively short was observed by KLEBS in *Haemanthus puniceus*; it is also true for *Amaryllis*.

NERINE BOWDENII

Seed - spherical, diameter less than 1 cm. It is soft, fleshy (the food reserve is starchy) and chlorophyllous, protected by a thin layer of cork-like cells. SCHLIMBACH (110) comments on the stomata in the covering layer. Embryo small and poorly differentiated.

Germination - as before. The seed is pulled above ground by the stalk portion of the cotyledon. Some seedlings show the "worm-like" twistings and elongation which FISCHER (43) first noted for *Crinum*. The radicle is less well developed than in *Haemanthus* which is comparable to *Nerine* with regard to bulk, if seedlings of the same age are considered.

Anatomy.

Five strands run through the cotyledon, arranged as a mid-rib and two pairs of lateral strands. At the base of the sheath, the mid-rib divides, one half fusing with each of the two adjacent lateral strands. The cotyledon strands enter the central axis at different levels, giving the appearance of a slow transition, although, externally, no hypocotyl can be distinguished. The primary root is pentarch. There is a much swollen exodermis. As in other seedlings of this group the root becomes contractile.

LITERATURE/

LITERATURE ON SEEDLINGS OF
BULBOUS AMARYLLIDACEAE

Although germination is only referred to, the work of SCHLIMBACH (110) on the seed and embryo raises some points of interest. He finds a wide range of characters throughout. The majority of seeds have an excessive water content (e.g. *Crinum* 92.9%, *Haemanthus* 86.3%) and notes that such a high water content is correlated with a small, poorly differentiated embryo, requiring some time for after ripening. The converse is true. KLEBS has little to say on the seedlings; the root of *Haemanthus* is one of the few organs of which details given. The work of BRAUN, FISCHER, SALISBURY and WORSELY on the bulbiform seeds and the germination of *Crinum* has been mentioned. Members of the family studied by SARGANT were not bulbous. The only anatomical study on a bulbous plant at the beginning of its history was done by TAYLOR (120) and FARRELL on *Cyrtanthus*. The latter from an examination of the embryo of *C. sanguineus*, stated that the sheath of the Monocotyledon is a fusion of two or more seed-leaves; since, of two structures (each formed by the merging together of two outgrowths) one aborts. There are four vascular strands in the sheath, but two higher up. TAYLOR/

TAYLOR, however, finds in *C. parviflorus* a terminal structure and remarks that the seedling anatomy connects easily with SARGANT'S Amaryllidaceous types.

DISCUSSION/

DISCUSSION

(a) Both families hold the following features in common.

- i. Bulb formation, which is apparent within the first two months of life.
- ii. A strong primary root which may function alone for a year. Reinforcement by adventitious roots is strictly limited and root hairs are produced sparingly. During the first year only one cauline root, as a rule, appears. For the purpose of secure fixation of the bulb in the soil, the radicle becomes contractile. In each case, there is modification of the cortex for the purpose of water storage; the second group of the Amaryllidaceae show further elaboration in the form of an enlarged exodermis or a multiple piliferous layer. The continued elongation of the radicle is doubtless related, not only to its pulling and anchoring function but to the habit of plants so highly specialised for unfavourable conditions. Here, as in the succulent group/

group, deep boring roots are a real necessity.

iii. The absence of hypocotyl was observed in the seedlings dealt with and commented upon in the literature of *Erythronium* and *Crinum*, and is in direct contrast to seedlings of these families, having a different habit, e.g. *Doryanthes*, an Amaryllidaceous arborescent plant, has a seedling with lengthy hypocotyl. Naturally, as the plumule is below the surface and tends to be pulled deeper, a hypocotyl would be superfluous.

iv. Heavy cutinisation of the epidermis of both cotyledon and foliage leaves for the conservation of water.

v. KLEBS Type V. for germination.

(b) With regard to the last point, although germination can be referred to a central type, details may vary. The tendency in the few publications on this aspect of seedling morphology, seems to be to magnify the divergences rather than co-ordinate types of germination, which at first sight seem to be widely digressing. CHOUARD (25) has made a key for recognition of certain members of the Scilleae/

Scilleae on a basis of these variations and ARBUR (3) figures fourteen Liliaceous seedlings merely to show how different from each other they apparently are.

The germination of the bulbous group may be summarised as follows:-

- A. The cotyledon is an aerial photosynthetic organ, lifting up the seed on its tip. Germination may be slow, when the cotyledon alone functions as an organ of Assimilation, e.g. *Bowiea*. CHOUARD notes this type as characteristic of *Scilla*, *Muscari*, *Bellevalia* and *Hyacinthus* in the tribe Scilleae. On the other hand germination and rate of development may be rapid in which case the first leaf develops early. The cotyledon sheath may be short, as in the majority of the above cases, or relatively long.
- B. The cotyledon remains underground but still has the form of Type V. In pickled material where the plants have lost their chlorophyll it is difficult to decide whether the seedling belongs to this or the A. type. The cotyledon differs in two respects from that of the above group; it is not photosynthetic and instead of elongating/

elongating to carry the seed upwards, it assists the primary root in forcing the plumular bud at its base, deeper in the soil. *Lachenalia* and the majority of *Amaryllidaceae* fall under this heading. As would be expected, plumular development is fairly rapid and there is a good store of endosperm to compensate for the loss of food manufacture by the cotyledon.

(c) Variations in the nature of the cotyledon.

i. As already noted, it may be above or entirely below ground, with a long or short sheath.

ii. It is cylindrical as a general rule.

Lilium and *Nomocharis* have a cotyledon the central portion of which flattens to give a bigger surface.

iii. In each case its base forms the outermost scale of the bulb.

iv. The abnormal development and activity of the stalk portion in certain of the *Amaryllidaceae* has been referred to.

(d) When the anatomy is investigated, the main differences are revealed. The *Liliaceae* considered have/

have two strands in the cotyledon, (except Erythronium which has three) and the root stele is di- , tri- , or tetrarch, pentarchy being unusual. The vascular anatomy of Amaryllidaceae does not show this uniformity as the following brief summary will show.

	<u>Cotyledon</u>	<u>First Leaf</u>	<u>Root</u>
Hippeastrum X _____	2 strands	3 strands	3-arch
" bicolor _____	3 "	3 "	3-arch
" advenum _____	2 "	3 "	3-arch
Narcissus _____	2,+2 later- als	1,+8 later- als	4-arch
Pancratiun foetidum _____	2,+2 "	3 strands	4-arch
" maritimum _____	2 strands	3 "	4-arch
Zephyranthes sp. _____	3 "	3 "	3-arch
Brunsvigia K. 64 _____	6 "	9 "	6-arch
" K. 59 _____	9 "	9 "	10-arch
Clivia K. 101 _____	6 "	9 "	7-arch
" miniata _____	10 "	9 "	10-arch
Crinum K. 34 _____	6 "	5 "	6-arch
Haemanthus sp. _____	6 "	8 "	4-arch
Nerine Bowdenii _____	5 "	5 "	5-arch

The seedlings fall naturally into two groups.

- i. Those with two or three strands in the cotyledon and triarch or tetrarch roots, and which are/

are comparable to the Liliaceous group not only in this respect but in their external morphology, the size and appearance of seed and seedling being so much alike as to make them difficult to distinguish. This group is RENDLE'S first, in which the seeds are many but small.

- ii. The group having large, fleshy bulbiform seeds, equipped for rapid germination and, as the table indicates, with an internal structure corresponding to a development on a large scale, of embryo, cotyledon and plumule. The numbers more than suggest the intimate relation between root and cotyledon, which is scarcely influenced by the fluctuations in the number of first leaf vascular strands. While the latter will undoubtedly affect the strength of the root stele, their presence does not seem to disturb its symmetry, as determined by the cotyledon.
- (e) The habitat is presumably similar for all these seedlings, since they have been chosen as showing a similar response to it, viz. the bulbous. The influence of the habitat ought, then, to act more or less uniformly on all. Consequently the striking/

striking difference in anatomy between the two groups can only be referable to a factor which does vary, namely the size of the seed. The Amaryllidaceae furnish the first instance in this study of a direct relationship between external and internal morphology of the seedling and size of the seed.

- (f) Since bulky seeds are first encountered in this group of bulbous plants, the question is now raised as to how far the volume and weight of such seeds contribute to the adoption of a subterranean life for the cotyledon. Evidence from other groups must, however, be considered before an attempt is made to answer it.

B. CORMIC AND TUBEROUS PLANTSL I L I A C E A ETribe ColchiceaeMERENDERA BULBOCODIUM (Colchicum
autumnale)

Seed - endospermic; approximately 3 mm. in length.

Germination - KLEBS Type V. with subterranean cotyledon; Ligulate.

Cotyledon - consists of:-

- i. sheathing base approximately 2 mm. long, and narrow;
- ii. ligule several times (about nine) as long as the sheath: the first leaf breaks through the aperture at the top;
- iii. a very short stalk between i. and ii. ($\frac{1}{2}$ mm. in length);
- iv. a suctorial tip, less than 3 mm. long, cylindrical.

Plumule - occurs at the base of the cotyledon which carries it well below the surface. It is well developed. The first leaf is long, narrow and cylindrical, and has a strong mid-rib and four lateral strands. The outer pair of laterals fuse together at the base of the leaf. The other strands remain distinct as far as the transition. Internodes in the seedling are very short and hypocotyl is absent.

Primary/

Primary Root - is approximately half the length of the aerial portion. It is strong and persistent, becoming contractile. It is assisted, early in the plant's development by cauline roots.

Anatomy. Two strands with protoxylem almost touching run from the tip of the cotyledon horizontally through the stalk. Each branches, sending a weak strand vertically upwards through the ligule (at the tip of which it dies out), and a strong strand vertically downwards. They approximate to a double bundle above and below level of stalk. The two strands move towards the centre and enter the axial stele when the plumular traces are reduced to three.

Hypocotyl. An arrangement of five distinct traces (two cotyledonary) continues through 70 μ .

Transition - swift, occurs within 80 μ . The metaxylem of all the strands moves to centre; protoxylem and phloem move peripherally (from three plumular traces) and are joined by that of cotyledon strands, the metaxylem of which has come nearer to that of others. The phloem becomes segregated into three groups.

Root. The metaxylem is in a plate in the centre.

Phloem/

Phloem is well developed; very little parenchyma in stele. The cortex is of the usual type.

Development of the Corm.

FABRE describes how the radicle, after elongating for some time, becomes stationary in growth and its upper part swells. The corm is evidently produced from lateral swelling of the hypocotyl, but the epidermis of the top of the root and the base of the cotyledon act as a protective covering for it; the continued growth of the corm destroys the cortex of the root in its neighbourhood. The cotyledon strand is diverted from its course by the outgrowth: no anatomical details are given. The elongation of the starch filled conical body downwards, and the origin of a bud, arising laterally in the basal part of the corm, are described. The bud for the next year continues to be carried deeper in the soil by the asymmetric growth of the corm functioning for the current season; RIMBACH commented on this abnormal method of fixing the corm more deeply each year, the roots taking no part in the process.

In the seedling two or more months old, connection with the cotyledon is broken, and, though the cortical tissue of the radicle disappears, its epidermis and vascular tissue persist in order to form part/

part of the protective sheath of the corm. When the cotyledon shrivels up, the tunic of the tuber is the first aerial leaf.

Tribe Allieae

BRODIAEA HYACINTHA VAR. LACTEA

Seed - 4 mm. long; strong black testa. Two seedlings were examined.

Germination - Type V. The plumular bud is carried below the surface. A slight swelling marks its position.

Cotyledon. The rather massive seed causes the cotyledon to bend slightly towards the tip. The first leaf breaks through the cotyledon where the bend occurs. The cotyledon may therefore be regarded as consisting chiefly of sheathing base (4.5 mm.) with a short inclined stalk (1 mm.) leading to the suctorial tip.

Primary Root - is the dominant organ, being strong, persistent and, proportionately, very long (20 mm. in the youngest seedling examined).

Plumule - well developed; longitudinal sectioning (Fig.)/

(Fig.) shows its contribution to the primary root.

Anatomy. The cotyledon is traversed by a double bundle. The root stele is diarch. SARGANT (103) refers it to the *Allium* type of transition (Fig.).

The origin and structure of the tuber of *Gloriosa superba* will be referred to in connection with its seedling anatomy. (See Climbers).

LITERATURE ON THE SEEDLINGS OF LILIACEAE WITH CORMS AND TUBERS

In addition to QUEVA'S publication on the seedling of *Gloriosa* and the work of FABRE and RIMBACH on *Merendera bulbocodium*, no other account of seedlings of this group was found.

I R I D A C E A E

This family provides the majority of seedlings of cormic plants. The seedlings examined offer so many points of similarity that only *Crocus* will be described in detail.

CROCUS

Crocus/

Crocus speciosus var. albus.

Seed - small, spherical.

Germination. Six months elapse before germination occurs and thereafter development is slow. MAW (89) mentions the lengthy time taken for the seed to germinate but gives no description either of the seedling or the initiation of the corm. The cotyledon is of the hypogeal, non-ligulate type, the stalk being short but the sheath of considerable length. The primary root is the only one present in most of the seedlings examined. In one instance a cauline root is produced.

The first indication of the development of a corm is the appearance of a small lateral outgrowth, conical in shape, pointing downwards, and arising at the base of the cotyledon on the side remote from the stalk and seed.

Anatomy of seedling showing development of the corm.

The cotyledon possesses a single vascular strand, which is evidently a greatly reduced double bundle. The first leaf which is of a simple cylindrical type, has four strands towards the base, but three near the tip. The second leaf has five vascular strands and shows/

shows the two invaginations responsible for the form of the adult leaf (3).

The cotyledon strand joins the plumular traces at a level where fusion of the cotyledon base and base of the first node is not quite complete, and where the base of the first internode is becoming swollen. The mass of vascular tissue is irregularly disposed towards the centre of the axis, but the cormic development is lateral though chiefly hypocotylar in its origin. The embryonic corm has no vascular tissue except that shared by the hypocotyl, the strands on the side nearest the corm being derived from the plumule. The primary root is in a more or less direct vertical line with the cotyledon strand. It is tetrarch. The lower part of the cormic body lies between the intact root stele and the root cortex which thus acts as part of its first protective layer.

At this stage of development the primary root is contractile.

The arrangement of the vascular skeleton to ensure that the corm is in communication with the plumular traces directly and the primary root less directly, recalls that of *Erythronium* where the dropper is in process of formation.

Crocus/

Crocus vernus. The cotyledon has a double bundle, and the primary root is diarch.

Crocus Skorpili. The cotyledon has a double bundle, as in the other species, but the primary root stele is pentarch.

The development of a corm is clearly exhibited by a seedling of *Melasphaerulea graminea* one month old, and by *Lapeyrouisia juncea*, approximately the same age. Seedlings of other members of this group were too young, when sectioned, to show the basal swelling, but the nature of the hypocotyl is similar to that of the species mentioned; the base of the first internode is wide; it merges into the hypocotyl imperceptibly. The strands of the latter are very strong, and somewhat scattered in each case. Figures of serial sections and the following table of anatomical data show the resemblances between them.

The description of the adult plant in several instances was taken from BAKER'S monograph on the Iridaceae. (5)

I./

	<u>Cotyledon</u>	<u>Vascular Anatomy</u>		
		<u>Cotyledon</u>	<u>Radicle</u>	<u>First Leaf</u>
I. <u>TRIBE - CROCOIDEAE</u>				
<i>Crocus speciosus</i> v. <i>alba</i>	Hypogeal, non-ligulate	2 strands	2 poles	3 strands
<i>Crocus Skorpili</i>	"	"	5 "	4 "
<i>Crocus vernus</i>	"	"	4 "	4 or 6 "
<i>Romulea ramiflora</i>	"	1	3 "	2 strands
II. <u>TRIBE IRIDOIDEAE</u>				
<i>Ferraria undulata</i>	ligulate	1	2 "	5 "
<i>Tigridia Pavonia</i>	ligulate	1	2 "	3 "
<i>Hexaglottis longifolia</i>	ligulate	1	2 "	6 "
III. <u>TRIBE - IXIOIDEAE</u>				
<i>Dierama pulcherrimum</i> v. <i>alba</i>	non-ligulate	1	4 "	5 "
<i>Gladiolus</i> sp.	"	1	3 "	4 "
<i>Ixia scariosa</i>	"	1	3 "	7 "
<i>Lapeyrouisia juncea</i>	ligulate	1	4 "	5 "
<i>Melasmaerulea graminea</i>	non-ligulate	1	2 "	5 "
<i>Watsonia</i> sp.	ligulate	1	5 "	7 "

LITERATURE/

LITERATURE ON THE IRIDACEOUS SEEDLINGS
OF THIS GROUP.

The seedling anatomy of Tigridia and Freesia was described by SARGANT. RIMBACH gives an account of the descent in the soil of the corm of Tigridia Pavonia. MAW'S observations on the crocus and KLEB'S comment on the absence of root hairs in the seedling of the same genus are the only references to the early life history of the Iridaceae in this group. RENDLE (96) notes the origin of the corm in Gladiolus illyricus.

A R A C E A E

There is to a certain extent uniformity in the germination for the members of the family. Accordingly only Arisaema will have its germination described with any attempt at detail.

ANTHURIUM SCHERZERIANUM

The early stages of germination are figured, but the anatomy and information on subsequent development are not yet available.

ARISAEMA/

ARISAEMAArisaema Jacquemontii

Germination. The radicle emerges from the spherical seed, carrying the plumular bud three to five mm. below the surface. Elongation of the sheath lifts the seed to the surface in some cases, but as a rule the cotyledon is subterranean. The tip of the cotyledon is cylindrical; it lies in a shell of endosperm, surrounded by perisperm. The sheathing base of the cotyledon may be 5 mm. in length when the total length of the seedling is only seven mm. The primary root is poorly developed, but the root cap is a prominent feature. The first leaf is differentiated into sheathing base, slender stalk, and heart-shaped lamina.

Anatomy. Four strands proceed from the tip of the cotyledon and are increased to five before leaving the seed to proceed through the sheath, at the upper part of which a line of weakness indicates where the slit will occur to free the first leaf when it is sufficiently long. The vascular system of the sheath may be regarded as a mid-rib and two pairs of lateral strands as SARGANT suggests for Arum, but in some cotyledons/

cotyledons of *Arisaema* only four strands occur. At the base one divides in two; another joins the plumular axis. The other strands do likewise, gradually forming three rays which converge centrally. These are joined by plumular traces, also forming three rays. The xylem becomes more compact, forming a central plate, flanked by two smaller patches. Lower it is surrounded by an endodermis and segregates into five poles. The radicle has therefore a pentarch stele. In another seedling in which there are four cotyledon strands, uniting with four plumular traces, the upper part of the stele is triarch but lower is diarch.

The widely spread ray formation of the vascular tissue in the hypocotyl possibly indicates preparation for tuberosity which is otherwise not apparent in seedlings of the age examined, when the first leaf had not yet emerged.

Arisaema concinnum.

The seedlings show marked tuberosity of the hypocotyl. Germination and general anatomy differed in no essential from those of *A. Jacquemontii*. The cotyledon strands do not join the plumular traces in the hypocotyl but proceed independently through the swollen axis (Fig. 60).

The/

The primary root persists for several months. Adventitious roots arise at the base and at the middle of the tuber.

Arisaema triphyllum

As many as nine strands may be found in the bulky tip of the cotyledon, but they reduce to four in the sheath. They run parallel for some distance with the plumular traces through the tuberous hypocotyl. The plumular traces form a crescent which, lower, breaks down. No definite hypocotylar stele exists at any level for the vascular supply is drawn upon to supply the primary and two equally strong adventitious roots. The primary root is triarch. A diarch adventitious root is supplied principally from first leaf traces. The three root steles arise about the level of the tuber's maximum diameter and proceed through a ground mass of starchy parenchyma (Fig. 59), each maintaining its own identity.

MCDUGALL describes in great detail the morphology of the germination of this species but not to the same extent the anatomy. He notes the delayed development of the plumule and the enlargement of the corm simultaneous with the production of the first leaf. Etiolation experiments showed that germination/

germination without development of the plumule had occurred. He found a central and two pairs of lateral strands in the cotyledon and triarchy in the radicle.

Arisaema intermedium.

Sections were made through a tuber six months old. The only trace of the cotyledon was the scar left where the upper portions had been cut off by periderm. The outer protective layer was doubtless cotyledonary: it consisted of periderm six cells deep. The covering of tuber is spotted with a red pigment. The tuber stores starch. A longitudinal section of the tuber shows five leaves forming a conical apex, and apparently only scale leaves. In the centre of the tuber a massive stele is surrounded by five or six smaller root steles. Roots may arise towards the top of the tuber (Fig. 60).

SARGANT records seven to nine bundles in the cotyledon and a triarch or tetrarch root for the seedling of *Arisaema speciosum*.

ARUM

Arum hygrophilum

Germination - as for *Arisaema*. The primary root is remarkable/

remarkable for its length and powerful nature.

Anatomy - similar to *Arisaema*. Six strands are found in the cotyledon. The hypocotyl exhibits the scattered arrangement already seen in other tuberous seedlings, though the strands are weak. The primary root is pentarch.

Arum italicum - as for *A. hygrophilum*. The cotyledon, however, has seven strands towards the upper part of the sheath where the slit occurs, although there are only six at the base of the sheath.

RICHARDIA ELLIOTTIANA

Seed - is five or six mm. long. It has a ribbed testa, and is three or four times as large as that of *Arisaema*. A remarkable production of adventitious roots occurs in the young seedling.

Anatomy. The cotyledon tip is cylindrical, occupying half the diameter of the seed. The conducting tissue towards the distal end of the tip is radially arranged, with three arms of vascular tissue proceeding for a short distance from the centre. Nearer the micropyle the arrangement is in the form of a hollow cylinder with two gaps, the xylem forming the inner/

inner, and the phloem the outer ring. The sheath has a double bundle and four pairs of lateral strands.

The first leaf has a mid-rib and three pairs of laterals, which, with the primordia of the second leaf, contribute four traces to the hypocotyl at a level where the strands of the cotyledon are fusing in adjacent pairs only the mid-rib pursuing its course unaltered. Fusion between cotyledon and plumular strands does not occur in the hypocotyl. The root stele is made up principally of cotyledon strands, the central double bundle being responsible for one root pole. The root, throughout its length is hex-arch and, in view of the proportions of seed, cotyledon and plumular bud, is poorly developed.

LITERATURE ON THE SEEDLINGS OF AROIDS

The germination of Aracea is represented in LUBBOCK by that of Anthurium, while KLEBS mentions two species of Arum in his Type I.

The first thorough investigation of general morphology, detailed anatomy and developmental stages of an Aroid seedling appears to have been made by SCOTT and SARGANT in 1898 on Arum maculatum. They were impressed by the extraordinarily slow growth of the seedling/

seedling, the first ovate leaf appearing as late as in the third year of growth. The structure of the seedling is similar to what has been described for Arum. *sp/* The production of the tuber, emergence of roots from the upper surface of the latter, cutting off of the cotyledon by periderm, lack of chlorophyll during two seasons, are described. Since the tuber shows no root structure it is assumed that it belongs entirely to the stem, while the formation of a vascular girdle at the nodes, characteristic of the adult, is shown in the youngest seedlings. No part of the hypocotyl shows the character of a true stem. There are five strands in the cotyledon, while the radicle has a tetrarch, passing into a triarch stele. In a later paper (103) SARGANT, in producing evidence for the double bundle theory, states that the peculiar habit has modified the vascular system of the cotyledon and suggests that *Anthurium Bakerianum*, with a single double bundle from the cotyledon, in its transition, is more primitive than *Arum*, a line of succession from *Anemarrhena* through what she considers transitional forms in the Liliaceae to *Zygadenus* and *Anthurium* being given.

CAMPBELL published from 1900 onwards a series of studies on the Araceae. He considers that the embryonic and post-seminal development of certain genera indicate/

indicate primitiveness. The lateral development of the primary root of *Lysichiton camtschatcense* suggests Isoetes to him. The preponderance of cotyledon and very slight differentiation of primary root in the embryo was characteristic also of *Aglaonema* and *Spathicarpa*. Of *Anthurium violaceum* he notes that "like other low monocotyledons, the embryo is far advanced when the seed is ripe" *Nephtytis liberica* has an embryo 1 cm. long, the greater part of the mature seed, but root and stem are "relatively poorly developed".

MACDOUGAL compared seedlings of *Arisaema triphyllum* and *A. Dracontium*, discovering that like *Arum maculatum*, the latter was saprophytic in the first season of its development, though its corm, in contrast to that of *Arisaema triphyllum*, develops before the plumule emerges. Only 10% of the plumules of the examined seedlings were functional, and these tended to degenerate. He concluded that *A. Dracontium* is losing its power of producing a normal assimilatory plumule, though its highly organised hypocotylar vascular system, of little service to a seedling without a plumule, is retained. The type of germination is of no service to the plant; it is actually disadvantageous. Its cormic development is the "expression of an inherent tendency to carry the young/

young plantlet as far as possible in its development before an assimilatory organ is produced".

In 1904 CHRYSLER chose the Araceae to illustrate the development of the central cylinder. In the section dealing with Aroideae he expresses the opinion that the peculiar habit of sprouting may have modified the vascular tissue in *Arum italicum* which is a "highly organised" seedling with "no suggestion of primitiveness". As for *Arisaema* "the phylogenetic development of the corm has been accompanied by changes in the vascular system".

A. W. HILL (1906) believes that *Arum* and *Arisaema* are allied to the Piperaceae and not far removed from a Dicotylous ancestry, but *Anthurium*, due to xerophily, shows analogies to a more ancient group of Lilies with the simplest forms possessing a single bundle in the cotyledon and the most ancient forms possessing a double bundle. The Aroids are a more primitive and less highly specialised group than the Liliaceae.

GATIN'S contribution (52) to the embryonic and seedling anatomy of the group is extensive in its scope. He concentrates on the morphology in the ripe seed and at the initial stages of germination. The following genera are dealt with - *Pothos*, eight species of *Anthurium*, *Acorus*, *Spathiphyllum*, *Aglaonema*, *Nephtytis*, *Dieffenbachia*, *Zantedeschia*, *Caladium*/

Caladium and four species of Arum. In several instances germination was not observed. His conclusions are of sufficient interest to summarise.

1. Embryo

- (a) Is proembryonic in Caladium, little differentiated as in Spathiphyllum, more highly differentiated in the others.
- (b) Is in an albuminous seed in the case of Anthurium, Spathiphyllum, Zantedeschia and Arum.
The seed of Aglaonema, Nephthytis and Dieffenbachia is exalbuminous.
- (c) The peripheral protection of the embryo differs. It takes the form of secondary suberisation in Aglaonema, Nephthytis and Dieffenbachia, but is epidermal in the others.
- (d) A central bundle is typical for the cotyledon of Anthurium and Spathiphyllum. The anatomy is variable according to the level in Zantedeschia and Arum. In Aglaonema the vascular strands are in an almost continuous ring. In the rather similar Nephthytis they are isolated.

2. Germination. The digestion of the albumen in the seed by the suctorial tip is mentioned. The primary root may be absent, its place being taken by laterals already formed in some cases in the seed. Two plumules are found in Nephthytis liberica and Aglaonema and two plants develop in a solitary sheath united by one cotyledon, an anomaly which GATIN discovered also in Palms. He describes the germination of Anthurium pedatoradiatum as "admotive", i.e. ligulate, if the word has/

has the same significance as in his former (48) paper "The embryo produces a large root and plumule which escapes by a slit and is enveloped at the base by a slightly developed ascending sheath. The root is covered by numerous absorbing hairs". This description also fits the germination of *A. Scherzianum* in which the early developing plumule is sheathed by the base of the cotyledon, which does extend upwards but does not produce a true ligule. No observations were made by GATIN on other species of *Anthurium*, of which he examined the seed.

EBERLE, in his research on a few Araceae, concentrates on the formation of the tuber, rather than on the seedling, but his observations on *Saurum* and *Amorphophallus* make an interesting comparison with what has already been recorded. Growth is sympodial, the tubers consisting of shortened internodes; the first foliage leaf is actually the thirteenth leaf organ.

The most recent publication on an Araceous seedling seems to be BOODLE and HILL'S account of *Typhonodorum Lindleyanum*, a viviparous plant of the swamps. The main portion of the young embryo consists of a dense corm-like body on the upper side of which the plumule lies while from the lower side a peg-like/

peg-like haustorium develops. The corm-like body which grows up round the highly advanced plumular bud is regarded as a specialised portion of the cotyledon or a lateral hypocotyledonary outgrowth. In water the corm-like body acts as a float in addition to its food storing capacity; the spongy haustorial organ has a secondary function in enabling the young seedling to float vertically. The only comparable case is that of *Cryptocoryne* which GRIFFITH described in 1847 under the name of the *Ambrosina ciliata* of ROXBURGH. In this instance the young plant when liberated into the water consists of an upper plumular part, very short stem and root rudiments, and a lower part which is the haustorial cotyledon; the latter organ soon breaks away from the rest of the plant. *Typhonodorum* retains the cotyledon. The first three to six leaves are all petiole. After rooting, succeeding leaves develop a lanceolate or ovate lamina, and later the mature form. Regarding *Cryptocoryne*, GRIFFITH remarks that the highly developed plumule obviates the necessity for the cotyledon.

D I O S C O R E A C E A E

TAMUS COMMUNIS

Although seedlings were examined, no microtome sections/

sections were made, QUEVA having fully described germination and anatomy.

The embryo has neither root, nor stem axis, nor any trace of a tuber. The lower part of the hypocotylar axis gives the first indication of it shortly after germination. The primary root is triarch. It is inserted on the anastomosing fibro-vascular mass that results, in the hypocotyl from the union of plumular and cotyledon strands. The cotyledon has only one strand and is composed principally of a sheath. The hypocotyl is exceedingly short. The tuber is at first a lateral outgrowth on the "dorsal face" of the hypocotyl, i.e. it is produced on the side remote from the seed. It receives the primary strands inserted on the hypocotylar vascular system. In later stages it elongates downwards due to the activity of a positively geotropic growing point. Two zones of cambium form; the inner zone produces fundamental tissue and secondary vascular tissue; the outer cambium lays down cork. The tuber at this later stage is an organ resulting from hypertrophy localised in the hypocotylar axis, but also involving the two first internodes. According to QUEVA, it is anatomically a stem, morphologically it has the exterior of a root, and physiologically is a great mass of tissue acting/

acting as a food store.

TESTUDINARIA SYLVATICA

Longitudinal sections show the origin of the tuber to be similar to that of *Tamus*. The primary and adventitious roots appear in older seedlings as if growing obliquely from the upper part of the tuber. The seed is flat and winged. It adheres to the suctorial tip of the cotyledon for a considerable time.

TESTUDINARIA ELEPHANTIPES

Germination and type of seedling as before. Tuber formation had begun, in the youngest plant examined (7 weeks old), by which time the lamina of the first leaf had almost expanded. There are curious hairs on the petiole of the latter (Fig. 67). The primary root which is triarch is poorly developed for the size of seedling. The seed persists for several months, the cotyledon tip being a rather lengthy, slender cylindrical organ.

QUEVA reduces the tubers of *Dioscoreaceae* to four types:-

- (a) The *Tamus* type, the origin of which has been referred to, is traversed by secondary vascular tissue/

tissue save for a few small hypocotylar strands.

- (b) The *Helmia* type arises by hypertrophy of the base of the primary stem and the hypocotylar axis. The tubers are annual and the vascular system primary. Morphologically they are more advanced than those of group (a).
- (c) The type illustrated by *Dioscorea Kita*, the tuber arising from the hypertrophy of one side of the hypocotylar axis.
- (d) Tubers which are "rhizomatous" produced from an axillary bud of the second leaf.

DALE described the origin of the aerial tuber in *Dioscorea sativa* L. , remarking that it belonged to DE BARY'S third category of underground tubers in which leafless tubers are produced by the swelling of the first epicotyledonary internode of the seedling.

DISCUSSION

- (a) The indications of corm or tuber formation within the first six weeks or two months is a common feature. No distinction was made between corm and tuber. In the Iridaceae the term corm is given to the perennating body, which is renewed annually. The name tuber is commonly used of it in the Araceae, although several writers apply the word corm to the underground organ of *Arisaema*.

(b)/

(b) The origin of the corm or tuber is by no means the same in every case.

- i. In *Merendera* it arises as a lateral swelling of the hypocotyl although the upper part of the root is also involved in that it acts, with the base of the cotyledon, as a protective covering. The descent of the corm in the soil is peculiar.
- ii. *Gloriosa*, another Liliaceous genus, has a tuber which is produced by the swelling of the primary stem, beginning above the second node, and extending to the base of the third internode, sheathed by the bases of the first and second foliage leaves.
- iii. In the case of *Crocus*, *Lapeyrouisia* and *Melasphaerulea* the cormic development is lateral, arising from and below the base of the first node. It is therefore hypocotylar in its origin. It is protected by the epidermis of the sheathing base of the cotyledon and the hypocotyl. The epidermis of the upper part of the root is displaced outwards and sheathes the lower part of the embryonic corm.
- iv. RENDLE (96) states that the corm of *Gladiolus illyricus* arises during the first vegetative season by thickening of the internode above the insertion of the first leaf. It is at first surrounded by the thin sheath of the cotyledon which, however, soon disappears while the sheath of the succeeding foliage leaf forms a dry membrane round the corm.
- v. The Aroids produce their tubers by the storage of food reserve, usually starch, in the hypocotyl. The vascular supply of the tuber in the first instance is therefore the original hypocotylar traces of the seedling. The first internode or the upper portion of the radicle is not involved in the tuberosity.
- vi. QUEVA'S classification of Dioscoreaceous tubers has been summarised. The tubers of this family may originate from hypertrophy of/

of the hypocotyl and the two lower internodes (Tamus, and some Dioscoreas), from hypertrophy of only one side of the hypocotyl (Dioscorea Kita), or from an axillary bud of the second leaf. The production of two zones of cambium in many of these tubers has been noted.

- (c) GATIN'S work on the embryo shows that the seed in the Aroids is not constant in its structure at maturity, being albuminous in some and not in others. Where the plumule is late in development the endosperm is directly responsible for the increase in volume of the corm or tuber. Data are not available for the size of seeds of plants referred to in the literature, but, among those actually examined, the seed of Merendera and Iridaceae were the smallest. Seeds of the Dioscoreaceae were only a little larger than these, if the membranous wing be allowed for. The Aroids had in general the largest seeds, though there is little appreciable difference between those of Crocus and Arisaema, to take two examples, at random, both albuminous. Size of seed cannot then be regarded as a factor involved, when considering differences of seedling structure for the group.
- (d) Type of germination is variable, all forms being found./

found. The only constant feature is that the cotyledon is always subterranean for most of its length. In odd cases the seed may be lifted a millimetre or so above ground, but this is exceptional. In considering the frequency with which the ligulate type occurs throughout the group, it will be recalled that out of thirteen Iridaceae only four had ligulate cotyledons; *Merendera* and *Gloriosa* in Liliaceae furnish the only additional examples. The aroids are without exception non-ligulate. GATIN evidently considered the slight upward prolongation of the sheath of *Anthurium* a true ligule, but it is by no means the closed tubular structure seen for example in *Merendera* being exactly similar in external morphology to the sheath of the *Aloe* cotyledon. GATIN observes of *Anthurium* that "l'embryon contient un plantule dont l'axe est courbe" and figures such an embryo but applies no adjective to the type of germination, while of *Anthurium pedato-radiatum* he says that the germination is adnate, but gives no information regarding the embryo. These findings will be discussed after the Palm group has been described.

- (e) CAMPBELL'S and GATIN'S researches on the embryo of the Aroids have revealed instances of embryos with very poorly defined tissues. It is interesting in this connection to recall the undifferentiated embryo of the slowly developing "tuberous" seedling of *Paris polyphylla*. GATIN has pointed out that there is a gradation in the differentiation of the embryo. Since he could give no facts regarding the germination of *Caladium* and *Spathiphyllum*, the embryos of which are most ill-defined in their parts, no comparison can be made for the purpose of correlating embryonic structure with tuberosity of the seedling, marked or otherwise. Tuberosity is not indicated however in the embryo. In MACDOUGAL'S study of *Arisaema Dracontium* delayed germination is associated with early tuberosity, and MAW remarked on the six months required for *Crocus* to germinate, an observation confirmed personally.
- (f) The plumular development affords an interesting study. Amongst the Araceae it is most backward; in *Arum maculatum* which requires three seasons to produce an aerial leaf. Several of the *Arisaemads* possess a corm before the first leaf is set free from the cotyledon sheath and the general rule is that/

that this is the only photosynthetic organ functioning for the first season. The plumule of *Merendera* was so poorly differentiated that FABRE hesitated to call it "a plumular bud". On the other hand, the development of the corm not only begins early but its progress is more than usually rapid. X

Seedlings of the Iridaceae whether of cormic or rhizomatous plants, have more or less the same plumular development and rate of progress. Their aerial parts are not confined in the first year to one leaf. The Dioscoreaceae, however, agree with Araceae in having a solitary leaf during the year of germination.

The differing degrees of plumular development indicated above cannot be the result of the morphology of the cotyledon, for in the Iridaceae, the only section with ligulate and non-ligulate types, such development is fairly uniform, nor can it be due to the position after germination of the cotyledon which in every case is hypogeal. In extreme cases of delayed development it is apparent that the corm or tuber is enlarging at the expense of other organs of the seedling, a procedure which is advantageous, according to MACDOUGAL/

MACDOUGAL for a reason already mentioned.

Two of the three exalbuminous seeds described by GATIN produce embryos with two plumular buds, a phenomenon which would have to be considered, not only in connection with the exalbuminous state but with the undifferentiated state of the embryos themselves.

- (g) Nature of the First Leaf. In *Crocus*, *Romulea*, (*Iridaceae*) *Nephtytis*, *Cryptocoryne*, (*Araceae*) and *Dioscorea repanda* the first leaf is reduced to a sheath. In *Anthurium* the first leaf has a reduced limb but the second the lanceolate form. In *Arisaema* and the remainder of *Araceae* examined as well as in the family *Dioscoreaceae*, the first foliage leaf is differentiated into sheath, long petiole and cordate net-veined lamina. Thus, though the plumular development may be said to be poor with regard to the number of leaves, the single leaf above ground is extremely efficient. While it may be without real significance it is worthy of note that the photosynthetic cotyledon of *Paris*, functioning alone in the first season, has the same form of petiole, lamina and venation.

- (h) Anatomy of the cotyledon. The *Liliaceae* have a double/

double bundle in the cotyledon. In Iridaceae there may be a single bundle, a double bundle (SARGANT records a mid-rib) and two lateral strands in Freesia sp. In the few Dioscoreaceae for which information is available, there are two strands. Larger numbers are found in the Aroids. Richardia has a mid-rib (a double bundle) and eight lateral strands, Arum six or seven strands, Arisaema four or five strands. The number is variable even in a species.

- (i) Hypocotylar anatomy is on similar lines for all. The vascular strands, usually numerous, are on a scattered plan, but anastomes are frequent. The structure in no way resembles the typical root, but the tendency for centralisation of the strands prevent it from having the characteristics of a stem. Its structure is one well fitted for an organ which in the course of development will swell.
- (j) The anatomy of the primary root offers no peculiarity. Diarchy, triarchy and tetrarchy are common. Only Arum, which had seven cotyledon strands is pentarch. Richardia is the sole example of a seedling with hexarchy in the root and this species had the most numerous cotyledon strands. There is/

is an obvious relation then between number of cotyledon strands and number of poles in the root. This was indicated further by the two seedlings of *Arisaema triphyllum* in which the root poles increased with the number of cotyledon strands.

The root system suggests that it is a compromise between that of bulbous and of rhizomatous seedlings, for the radicle becomes contractile as in the former groups but is early reinforced by numerous ^{cauline} ~~primary~~ roots. In a seedling two months old, it is difficult to determine which is the primary root for at that age at least one other contractile root is equally developed, and in addition three or four thin roots, purely for nutritive purposes, are present.

While the radicle is lengthy in the majority of cases, it may be poorly developed or, in rare cases, missing, in the Araceae and Dioscoreaceae. In *Arum maculatum* it persists for a year.

C. RHIZOMATOUS.L I L I A C E A ETribe AsphodeliaePASITHEA COERULEA

Figures

Seed - 3 mm. long. Roughly pyramidal in shape.

Germination - Type V., with subterranean cotyledon.

Development, which is rapid, involves equal rate of growth for root and shoot.

Cotyledon consists of:-

- i. broad, fleshy, sheathing base,
- ii. an extremely short, stout stalk,
- iii. a barrel-shaped suctorial tip.

Two vascular strands run throughout its entire length.

Plumule - well developed from the first. A seedling three days old has three leaves and the primordia of the fourth differentiated. One side of the seedling has had to extend in length faster than the other in order to fix the plumular axis vertically in soil; hence the first nodes are oblique. Internodes are short. Plumular bud actually 1 mm. or so below the surface. The first leaf is linear. It has no mid-rib but six parallel strands.

Hypocotyl - is very short. There is a difference of 100%.

100 μ between the levels where the cotyledon strands enter the axis, due to the obliqueness referred to. The xylem assumes a radial arrangement immediately the second strand fuses with the axial strands. An endodermis ensheathes the stele completely 60 μ lower.

Root. Primary root stout, strong, covered with root hairs, persistent. A collar of 3-4 layers of sub-epidermal cells occurs at soil level at the upper limit of the root only noticeable in young seedlings. The root stele has a remarkably wide endodermis and exceedingly well developed phloem. Vascular strand tough and stringy when root cut. The stele although medullated is very compact, there being a single pericyclic layer and very little phloem parenchyma.

Anatomy of transition. The plumular traces are reinforced first by the two pairs of laterals from first leaf, and at this level are joined also by one cotyledon strand, giving a ring of xylem (five patches) associated with phloem. The radial arrangement is not perfect. The strand formed from the two main traces from the first leaf becomes horizontal and joins with the stele at the same time as the second cotyledon strand does so (40 μ lower). This results in a stele with five phloem patches arranged between/

between three arches of xylem; further disintegration of the latter into four, then five rays occurs, giving a pentarch root stele (one-fifth of total diameter.)

ARTHROPODIUM CIRRHATUM

Seed - as in Pasithea.

Germination - Type V. with an aerial photosynthetic cotyledon.

Cotyledon consists of:-

- i. very short sheathing base,
- ii. green cylindrical lamina merging gradually into
- iii. short suctorial tip.

Two strands proceed from the tip to the base of the cotyledon, the lower limit of which is not obvious, for it passes, without change in width, into a cylindrical region, free from root hairs, approximately 6 mm. long, which may be looked on as hypocotyl although its stele has root symmetry (Fig. 3).

The epidermal cells are heavily cutinised on the outer tangential wall at this stage.

Root. At the level where root hairs arise in a ring there/

there is an abrupt diminution in width. This may be taken as the upper limit of the root which, in four seedlings, was found to be triarch. There is a central intercellular space in the stele.

Plumule - very poorly defined. Its position is marked externally by a slight swelling, barely perceptible.

Transition - was not followed. SARGANT (103) refers it to the Allium type of transition and states that the root stele is ^{di}tetrarch (cf. above note on root). The Pflanztenreich states that the adult plant has a short rhizome, and swollen roots.

CHLOROPHYTUM STERNBERGIANUM

Seed - as for *Pasithea* re size and shape.

Germination - Hypogeal; elongation of the primary root is rapid and development continues at a steady, fairly rapid rate.

Cotyledon consists of:-

- i. very short slender suctorial tip,
- ii. remarkably long thread-like stalk. In a day-old seedling is only 2 mm. long but at the end of a week is 8 or 9 mm. long. It lies parallel/

Fig 70

parallel to the hypocotyl and the sheath of the cotyledon.

- (c) Short ligular portion - this is apparent from the beginning, as soon as radicle takes up a vertical position (is less than 2 mm. in week-old plant).
- (c) Short sheath - approximately same length as ligule, partly below soil. Very slender; lower limit difficult to determine except by sectioning; no swelling to indicate base of cotyledon.

Plumule - well developed. The first leaf makes its appearance above ground in a few days. It is linear-lanceolate with a mid-rib and two pairs of lateral strands.

Primary root - dominant organ of the seedling. In a day-old plant it occupies four-fifths of length of seedling. For 6 mm. below the level where the cotyledon base fuses to the axis a cylindrical region of uniform thickness extends. The epidermis continuous with that of cotyledon is smooth and entirely free from root hairs. Though apparently hypocotylar the anatomy reveals this to have a true root stele. At a level corresponding to that of the seed in soil, a prominent swelling occurs marking the limit of the hypocotylar region. From this level to the tip the root/

root is 8 mm. long and is covered with a dense coating of root hairs. In older plants the roots are of equal or greater length than the shoot.

The radicle soon produces strong lateral roots, and cauline roots arise in a ring at the base of cotyledon which becomes swollen and very strong. A month-old seedling has three secondary roots but no adventitious ones. When three months old it has three very stout cauline roots (each with long root-lets) in addition to the primary root. At this stage many of the roots show markedly what was indicated in primary root, viz. local swelling (affecting the greater part of the root in some instances) giving the appearance of long tubers. The swelling is due entirely to increase in size of individual cortical cells; the number of cells is approximately the same. The cortical zone is three or four times as wide as in the unswollen part and the stele almost double its original diameter. Increase in the number of protoxylem poles does not occur but the xylem, which formed a compact ring, disintegrates into rays with large parenchyma lying between metaxylem elements and, in the centre, forming a medulla. The function of the cortex is water storage; starch is absent.

Anatomy/

Anatomy of one-week-old seedling.

Cotyledon. One double bundle proceeds through tip and stalk. After the latter fuses to the sheath the strand ascends 0.8 mm. and branches. Its upward vertical course continues through 0.35 mm. in the ligule; it then dies out. Its downward vertical course is 0.87 mm. in length (i.e. it finishes only 70 μ below the level where fusion of cotyledon base and stalk occurred).

Plumule. The first leaf has a mid-rib and two pairs of lateral strands. The inner pair absorb the traces from the plumular bud. The cotyledon strand passes to the centre and, incorporating first the outer laterals, fuses with the inner laterals.

Transition. The phloem of the inner laterals moves peripherally towards that of mid-rib to give one phloem patch and partly in opposite direction towards the cotyledon strand to give two patches. The xylem does not move but remains in a compact triangular plate, the cotyledon and outer laterals of first leaf together contributing to one xylem pole. The change from stem structure with the cotyledon strand entering the hypocotyl to typical root stele occurs within 50 μ . At first the stele is sheathed in parenchyma, compact/

compact but unthickened. Within 1 mm. from transition a typical endodermal sheath occurs (hand sections of other seedlings confirm this). One seedling with ⁴⁵two-arch root was found.

Root. In the region free from root hairs the epidermal cells are very small, square and regularly arranged, with marked cutinisation on outer tangential wall. Exodermal cells are larger, square-shaped with outer tangential and radial walls thickened. Cortical cells are very large and isodiametric, the largest occurring in the middle of the cortex. As the primary root ages, it thickens and the xylem poles are increased to four or five. The xylem may be arranged in a ring with a medulla, or in a solid plate. Lateral roots and cauline roots are 5-8-arch.

TRICHOPETALUM STELLATUM

Seed - very small, 1 mm. long.

Germination.- Type V. with cylindrical photosynthetic cotyledon carrying the seed at its tip. The passage from cotyledon base to root is very obvious, on account of the swollen nature of the upper part of the root, even in a seedling only a few days old.

(Fig. X).

Anatomy/

Anatomy. Two strands in contact so as to approximate to a double bundle, run through the cotyledon. The primary root is triarch and has a wide and succulent cortex.

Tribe Hemerocalleae

HEMEROCALLIS

Hemerocallis spicata.

Seed - covered by a smooth black testa; large and heavy (6 mm. long, 5 mm. in diameter).

Germination - Type V. with a subterranean cotyledon which consists of a large club-shaped tip and strong sheath.

A small circular lid is broken off to allow emergence of the primary root on germination. The seedling presents no unusual feature save for the occurrence of a band of parenchymatous tissue at the base of the cotyledon sheath. The robust nature of the seedling is noteworthy.

Primary Root - very stout and persistent. Although devoid of lateral roots, it is densely covered by root hairs.

Plumule - well differentiated. Three leaves and a strong bud are found at the stage where the first leaf pierces the apex of the sheath. This it does at/

at the end of a week.

Older seedlings show that root and shoot systems develop at an equal rate, but in the initial stages the length of the radicle may be twice as long as that part of the seedling above ground (Fig. 73).

Anatomy

Cotyledon. Four strands follow a parallel course from the tip to the base of the sheath at which level they are inserted on the plumular traces one by one. Six strands were found in the cotyledon of another seedling.

First and second leaves have ten vascular strands, so that the vascular traces at the lower limit of the axis are very strong, forming a ring.

Primary Root - is pentarch; there is a wide water-storing cortex and a stout exodermis of very large squarish cells.

In the seedling with six cotyledonary strands the root stele was hexarch.

Hemerocallis nana. Exactly similar to *H. spicata* except anatomically.

Cotyledon - five strands in the tip and sheath.

First/

First Leaf - mid-rib with three pairs of laterals, with subsidiary laterals between each pair.

Root - heptarch.

Hemerocallis Forrestii. Seed more spherical and slightly larger than in *H. spicata* and *H. nana* (length 6.5 mm., diameter 6 mm.). Differs anatomically from two preceding species.

Cotyledon - there may be four, five or seven strands in the tip. In one seedling the stalk region between sheath and tip, which is almost non-existent, may be hollow like an unrolled leaf (Fig. 73). Seven strands run through the sheathing base. There are ten strands in the first leaf.

Root - hexarch.

PHORMIUM TENAX

Seed - flattened, covered with a black, thin testa, (Fig. 75).

Germination - as in *Hemerocallis*. The seedling is, however, long and thin. Further a slender thread-like stalk, 2-3 mm. long, connects the suctorial tip to/

to the long sheathing base.

Primary Root - persistent and fairly well developed.

A seedling whose shoot portion is 35 mm. high, has a radicle 10 mm. long.

First Leaf - has a mid-rib and two pairs of lateral strands.

Cotyledon - has two strands which keep apart even in the tip. They join the plumular traces some distance below the fusion of cotyledon and plumular axis.

The long internodes are a little unusual.

HOSTA COERULEA (= Funkia)

Seed - three sided, covered with a black testa which forms a membranous wing at the end distal from the micropyle. The seed is 3-5 mm. long.

Germination. The embryonic plant is spindle-shaped, 1-2 mm. in length with a few root hairs above the root cap at one end and a thin cylindrical sucker, embedded in endosperm at the other. Germination is similar to that of *Hemerocallis*.

The plumular development is strong; a week-old plant has three leaves differentiated, the oldest of these being in the act of piercing the apex of the cotyledon sheath./

sheath. At the same time a cauline root is forming above the first node and the primary root is 1 cm. in length. The sheath is only half this length. Seedlings III and IV and older plants show a hypocotyl 3-4 mm. in length. This appears to be the maximum length. The elongation of the hypocotylar region has the effect of pushing the seed upwards so that it lies at the surface, or a little above it, in two weeks time. At nineteen days after germination the second leaf has expanded.

Anatomy.

Cotyledon. The course of the cotyledon strand can be followed without sectioning: it proceeds through the entire length of the organ, diverges from the vertical, at a gentle slope, some distance below the first node, and, though in a central position, remains independent till rearrangement occurs at the upper limit of the hypocotyl. It is a double bundle, equivalent to two strands fused at the protoxylem.

First Leaf. The lamina of this and succeeding leaves are heart-shaped. At the base of the first leaf the two laterals on each side of the mid-rib unite with one another, thus reducing the leaf traces to three. Further union results in two strands which are joined by the cotyledonary strand at the base of the axis.

Hypocotyl/

Hypocotyl. It partakes of root structure in that the stele is surrounded by a thin-walled endodermis: the stele consists of two circular meristematic patches, chiefly phloem, derived from the plumular traces for the most part. The two patches are separated by a xylem band partly of plumular, partly of cotyledonary origin. With very little readjustment this stele gives the typical diarch pattern for the root, the upper limit of which is indicated by a ring of root hairs.

Primary Root - persistent. At first of equal, then, for a period, of greater, length than the aerial part of the seedling. The appearance of lateral and of adventitious roots coincides with the emergence of the second and succeeding foliage leaves.

BLANFORDIA MARGINATA

Seed - 4 mm. long covered by a dark brown testa, spindle-shaped.

Germination - KLEBS Type V. The seedling is very slender. Root and cotyledon are equally developed. There is a hypocotyl 2-3 mm. long. The primary root is persistent.

Anatomy/

Anatomy. There is a single collateral strand in the cotyledon, in which there are only four xylem elements. In the hypocotyl the xylem is placed in a band across the stele as in *Hosta*; there is an enclosing endodermal sheath. The primary root has a very weak stele, four small groups of xylem (with one or two elements in each) being arranged peripherally in it.

Tribe Medeolae

PARIS POLYPHYLLA

A full account of this plant has been given by the writer elsewhere (16). A brief summary will therefore suffice. Germination is a modification of KLEBS Type V, The seedling, arising from a small undifferentiated embryo (55) has a highly specialised cotyledon, which consists of:-

- i. a sheathing base: this is also a food storage organ,
- ii. a thin cylindrical petiole,
- iii. a broad, cordate, photosynthetic lamina, reticulately veined like the foliage leaves.

Development is extremely slow.

The cotyledon strands consists of a mid-rib and two lateral strands. They dominate the seedling to such/

such an extent that they remain vertical, whereas the weak plumular traces are oblique. With further growth of the hypocotyl, the latter incline more to the horizontal. The lateral strands of the cotyledon fuse with the axial stele 0.5 mm. below the level where cotyledon, mid-rib and plumular traces merge. The upper limit of the hypocotyl may be regarded as occurring where the fusion of the laterals takes place though SARGANT would place it at the higher plumular fusion saying that the lateral strands maintain their identity in the hypocotyl. In the hypocotyl the xylem is disposed in closed or open rings, buttressed outside and inside by phloem, the vascular tissue lying in a parenchymatous ground mass. The persistent primary root is triarch. As it tapers towards the tip the stele almost diminishes, becoming diarch and finally monarch. A cauline root is produced during the first year. The horizontal traces in a year-old seedling function as the vascular system of a monopodial rhizome with the plumule at the end of the first node: the base of the cotyledon and the hypocotyl comprise one half of the rhizome at this stage while the cotyledon strand still maintains connection with the plumule and radicle by a necessarily indirect course. "It was hoped that the slow ontogenetic/

ontogenetic development might reveal points of phyto-genetic value and the transition in a hypocotyl of measurable dimensions gives sections with steles reminiscent of the dectyostele and solenostele of Ferns. It is difficult to say how far these are the result of the tuberous nature of the hypocotyl".

TRILLIUM OVATUM

Thirteen seedlings were examined. In the rate and type of germination (Type V), size and nature of seedling, and the lengthy period taken by the seed to germinate, viz. a year, there is a very close similarity to Paris.

Cotyledon - resembles Paris in the following respects:-

- (a) differentiation into, and relative development of lamina, petiole and sheath;
- (b) rate and details of growth, e.g. unfolding and expanding of lamina;
- (c) is photosynthetic, the tip of the lamina detaching itself early from seed;
- (d) Is for a considerable period the only aerial organ of seedling;
- (e)/

- (e) there is a close resemblance in shape and veining between the cotyledon and first foliage leaf.

Plumule and First Leaf - slow in development. The bud is sheathed by cotyledon base in all seedlings examined. It appears as a small lateral protuberance towards the top of a very swollen hypocotyl which merges downwards into a thickened region, covered profusely with root hairs.

Seedling VIII. shows the first leaf emerging, bent at the juncture of petiole and lamina, the two, therefore, closely adpressed. Gradually it straightens out. Petiole and lamina are roughly the same length. The petiole is long, cylindrical and narrow; the lamina is lanceolate with a strong midrib and two parallel laterals; ramifications depart at two or three points from it to each side (Fig. 80).

Hypocotyl - lengthy. It is a storage organ (see anatomy). Its subsequent importance is indicated by its length in the youngest seedling.

Root. A stout root is provided from the first; though short at first it is very strong. Root hairs develop rapidly and the root elongates, becoming the dominant/

dominant organ (cf. Paris). It is long, straight and powerful and in some cases becomes contractile early. Neither lateral nor cauline roots appear until the first leaf is above the soil and the plant has a distinctly tuberous hypocotyl. (Seedling Fig. 81)

Anatomy of Seedling. Of six seedlings, whose roots were hand-sectioned, one diarch, two tetrarch and three triarch steles were found.

(a) Seedling with tetrarch root - (about three months old).

Petiole of cotyledon is triangular in cross-section; is traversed by a strong mid-rib, a double bundle (SARGANT) centrally placed, and two weak laterals. In young seedlings where there is no expanded lamina, this arrangement holds throughout the entire length of the cotyledon whose tip (about 1 mm. long) is imbedded in endosperm. In older seedlings the suctorial portion expands, on withdrawing itself from the seed, taking on the work of photosynthesis as it does so. In the lamina thus formed the three main vascular strands have ramifications so that a network extends to the tip. The petiole increases/

increases in girth as the sheathing base is approached.

The latter in addition to its work as a sheathing cylinder round the plumule is a storage organ. The double bundle and two laterals lie in a ground mass of large parenchyma containing starch. Intercellular spaces are few and very small. The first leaf evidently makes its way through the cotyledonary wall by rupturing it at its weakest point where there is a thickness of only two or three cells. No mechanism to assist in this was observed. Three strands (supplying first leaf) and a fourth strand (from second leaf and plumule) lying between them, pass from a lateral to a more central position descending through 0.2 mm. in doing so. At this level fusion occurs between the plumular and the three cotyledonary strands (contrast with the behaviour of the lateral strands of the cotyledon in Paris) which fuse with the axis at a level much lower than that at which the mid-rib does so.)

Hypocotyl - extends through 1.2 mm. and is the most swollen part of the seedling (diameter approximately 1.5 mm.). The epidermal cells are small, regular, with slight and evenly distributed thickening/

thickening on all walls, except the outer tangential wall which is more strongly cutinised. The sub-epidermal cells are similar in size and shape, unthickened and free from starch. The stele is enclosed in a sheath; lower this becomes better defined into typical endodermis with radially thickened walls. The diameter of the stele in the hypocotyl is roughly one fifth of the total diameter. The stele consists of six xylem masses lying in a tissue of phloem (poorly developed) and parenchyma. The protoxylem turns towards the periphery and fusion of two pairs of xylem rays reduces the latter to four patches.

The epidermis is now piliferous and the endodermis encloses a compact stele in which, however, the radial arrangement is not complete, and the xylem and protoxylem rather scattered. This piliferous region accounts for .3 mm. of the total storage region (2 mm. long). It is in this last fraction of a mm. that the xylem forms a plate with four arms, the phloem lying between the latter.

The cortical zone around the stele is free from starch for three or four layers. The remainder of the cortex stores starch. The layer of/
of/

of cells below the piliferous layer resembles that layer in size and shape of cells which contain no starch. The diameter of the root gradually diminishes towards the tip.

- (b) Seedlings with diarch and triarch roots. There is no essential difference in the anatomy. The cotyledon strands behave in a similar fashion as before, but the contribution from the plumule in the seedling with diarch root is less than for that resulting in a triarch root. There is the same scattered arrangement in the hypocotyl.

Development of the rhizome proceeds as in Paris.

In the very young seedling, the hypocotyl is out of proportion in width and length to the rest of the seedling. The swollen hypocotyl is found in the majority of seedlings. In some, however, (Fig. 81) it appears to be absent. The presence of copious endosperm still in the seed would account for or compensate for lack of food reserve in the hypocotyl. The preponderance of primary root in such seedlings seems to be correlated with this, also.

Ill-nourished seedlings, with no food store in the hypocotyl, throw up the first foliage leaf at/

at an earlier date than those with a well stocked hypocotyl.

As already noted, SARGANT (103) quoted *Trillium* as an example of the seedling anatomy of the *Medeolae*, but describes only the double bundle of the cotyledon with its pair of laterals. CHRYSLER (26) writing on the development of the central cylinder of *Liliaceae* finds that in *Trillium grandiflorum* the first leaves have three traces but after the fourth leaf forms, there is intrusion of the central cylinder by fundamental tissue. *Trillium* then, in his opinion, exhibits clearly the development of the stele in showing four stages -

- i. protostele;
- ii. siphonostelic stele with cortex forming a medulla;
- iii. segments of the stele becoming amphivasal;
- iv. strands becoming medullary and connecting with leaf traces.

It was mentioned in the account of Paris (16) that the work (which was complete before the writer had any knowledge of CHRYSLER'S paper) would furnish some points of interest in connection with the ontogeny of the stele. Had he investigated its structure, CHRYSLER would very probably have chosen Paris as an example in preference to even *Trillium grandiflorum* to/

to illustrate the above features. They are undoubtedly shown more convincingly by Paris than by *Trillium ovatum*.

The striking similarity between *Trillium* and Paris in the external and internal morphology of the seedling is interesting in another connection. GATIN (53) remarks that the trimerous varieties of Paris *quadrifolia* approach *Trillium* in the anatomy of the adult, that the three-leaved variety may be produced for several years before the four-leaved variety of *P. quadrifolia*, and thus the first type given is the ancestral type. FRANCHET (45) considers that *Trillium* leads to the three-leaved *P. quadrifolia* which may give the six-leaved European form and the Asiatic *P. hexaphylla*, thence *P. polyphylla*, or the European four-leaved *P. quadrifolia* and thereafter the five-leaved form and *P. obovata*. "The transformation of the primitive trimery into tetramery, then pentamery and hexamery has been effected and goes on still at the present day in proceeding from West to East in the Northern hemisphere". R. R. GATES (134) also discusses the variability of *Trillium* and its relation to Paris.

The extent to which this relationship can be traced in the early stages of the development of the individual has already been seen.

LITERATURE ON THE SEEDLINGS OF
RHIZOMATOUS LILIACEAE

SCHLICKUM describes the seedling of *Asphodelus luteus*. The germination is Type V. The young cotyledon has two strands: later its sheathing base has five strands. SARGANT gives the seedling anatomy of the following rhizomatous plants as evidence for the double bundle theory - *Anemarrhena*, *Asphodeline*, *Eremurus*, *Bulbine*, *Anthericum*, *Veratrum* and *Tricyrtis*. All have Type V. germination and a double bundle in the cotyledon. The roots poles are low in number, only two genera having more than four. CHRYSLER chooses several rhizomatous types in his study of the development of the central cylinder of Liliaceae, e.g. *Medeola*, *Polygonatum*, *Clintonia*, *Uvularia*, *Chlorophytum*, *Aloe*, *Anthericum*, *Anemarrhena*, but he is concerned only with the stelar anatomy, not with types of germination.

CANNACEAE

HEGELMAIER (56) and HUMPHREY (75) have described the seed and embryo.

Seed - spherical or egg-shaped, 8 mm. long. The testa is hard and thick. It projects into the perisperm forming a micropylar collar, by which part of the embryo is surrounded. The testa is provided with stomata. The bulk of the food store within is starchy perisperm, surrounding a thin aleurone layer, the true endosperm.

Embryo. At maturity it is remarkable for its high degree of differentiation, especially in the plumule which may have three clearly defined leaves, and rudiments of adventitious roots. It consists of two parts. The most conspicuous is the sucker of the cotyledon, a thick cylindrical organ ~~with~~ widening towards the rounded tip. A slight constriction separates it from the remainder of the embryo which is lying in the micropylar canal, enclosed in the collar provided by the testa, and which is not symmetrical. A projecting knob placed in a lateral position rests on the wall of the testa and this portion of embryo towards the micropyle seems to be bent. Sectioning shows that plumule and radicle do not lie in a straight/

straight line: their axes lie at an angle, hence the external appearance of the embryo.

CANNA INDICA

Germination. The radicle pushes out a circular lid which breaks off round a line of weakness in the testa. The earliest stage gives no indication of the type of germination. In a short time there is a strong ligular development on the part of the cotyledon. Fig. 83, shows a seedling the suctorial tip of which has been dissected out from the seed. It is a much swollen organ. A deep constriction has been made by the hard seed coat in the region of the germinal aperture. The portion of the seedling outside the seed is a spherical mass which does not suggest the position of the plumule within or the exact region of the root tip outside.

Anatomy of the mature embryo.

Cotyledon. In the tip which is 1.5 mm. in diameter twenty strands are arranged peripherally. At the constriction they unite until their number is reduced to four, five or six but it increases to seven or eight strands beyond this region, into the sheath. There are ten strands in the first leaf. Those strands/

strands which are on the side of the axis nearest the seed unite with the strands of the cotyledon, two leaf strands apparently fusing with each cotyledonary trace. At a level at which half of the cotyledonary strands are still independent, adventitious roots are initiated. A crescent of such roots arises at the level where complete union of cotyledon and plumular strands takes place. In view of this and of the fact that the angle between plumular and root axis now occurs, it was impossible to follow the transition which must be extremely rapid. For the same reason the structure of what represents the radicle cannot be determined. GATIN in his study of the embryo remarked that the primary root was endogenous in its origin. Even after germination, when the seedling might have given some information regarding it, the radicle is undeveloped and cannot be distinguished from the numerous adventitious roots of which there may be nine or ten, in its neighbourhood.

GATIN (49) figures the embryo and germination of *C. indica*. TSCHIRSCH gives a drawing of the longitudinal section through the ripe embryo. The former notes the large number of vascular strands in the cotyledon; fourteen are placed round the plumular bud, but the number of hypocotylar strands is eleven, lying in a half circle. SCHLICKUM (109) in comparing cotyledon/

cotyledon with the first leaf finds ten strands in the cotyledon sheath, ten or twelve in the first leaf and sixteen in the second leaf (Fig. <).

CANNA FLACCIDA

The seed, germination and seedling differ in no essential from those of *C. indica*. The ligular development of the cotyledon is less pronounced in *C. flaccida* (Fig. 83).

There are twenty strands in the suctorial part of the cotyledon but only five in the ligule. Fifteen strands with interlying aerenchymatous spaces are found in the first leaf which is a simple linear shape; the second leaf has a broad blade, tapering to a sharp point; it has seven main and eight subsidiary strands. A blunt projection indicates the end of the axis of the radicle although the nature of the radicle, if any, is impossible to discover. The section of an adventitious root shows a hexarch stele with very large metaxylem elements peripherally arranged, and a central air cavity. The endodermal cells are small and arranged with a regularity which is repeated by the inner half of the cortex, the cells of which are rectangular in shape, with rounded corners (Fig. 83).

CANNA SP. 301.

Seed and Seedling - as for *C. indica*. The same massive embryo (4 mm. long) is found. The ligule of the cotyledon is long (3-4 mm.) and thick. The suctorial tip has fourteen strands, arranged in pairs surrounded by endosperm, four cells deep, a tannin layer and copious perisperm. There are four or five strands in the ligule and four in addition in the sheathing base. Numerous adventitious roots arise on germination.

The first leaf is smaller than the second; they have eleven and thirteen strands respectively.

Z I N G I B E R A C E A E

The rhizomatous habit is common to all members of this family of perennial herbs, although the form which the rhizome may take is variable. Another constant vegetative feature is the occurrence of a ligule produced upwards from the long enveloping sheath of the foliage leaf. ENGLEr divides the family into -

- A. Sub-family ZINGIBEROIDEAE: Tribe I. Hedychieae
 Tribe II. Globbeae
 Tribe III. Zingibereae

B./

B. Sub-family COSTOIDEAE.

The distinction between the sub-families is shown by their seedlings in a very striking manner.

A. Sub-family Zingiberoideae

A general description of seed and germination will serve for the whole sub-family. The seed is spherical or almost so, and on the average is 4 mm. in length.

Seed. LUBBOCK takes *Elettaria speciosa* as typical; he mentions a lid-like stopper lying opposite the hilum which is pushed out by the radicle on germination and states that on the whole germination is similar for *Amomum* and *Alpinia*. No description of the seedling is given. HUMPHREY chooses *Costus* as a typical Zingiberaceous seed. This is unfortunate, for *Costus* is typical neither in its seed nor seedling. He remarks that "in the presence of the micropylar collar and germinal lid, and in the development of embryo and endosperm, all the forms examined agree closely" and quotes *Elettaria* sp. and *Alpinia nutans*, doubtless on LUBBOCK'S authority, as specific examples, although not figuring the ripe seed of either.

Costus of the sub-family Costoideae does possess a germinal lid. HUMPHREY figures the ripe seed of *Amomum*/

and
Amomum (Zingiberoideae) as having one, although the germination has not been followed from the initial stages, it can be seen that the stalk of the cotyledon emerges from the seed at a clean-cut circular aperture. *Alpinia calcarata* and all other genera of the Zingiberoideae examined during the present investigation show no trace of a germinal lid. The testa is ruptured along lines of weakness, running out from the hilum, so that a collar of five or six ragged triangular teeth edge the opening through which the radicle appeared (cf. *Billbergia*). The seed coat of *Roscoeia*, *Brachychilium*, *Hedychium* and *Alpinia* is the same as for *Costus*, which HUMPHREY describes. The outer integument gives rise to three layers namely an outer compressed lamina, thin and sclerotic, a very narrow nutrient layer, and an inner band of large cells, elongated radially, thickened on all but the outer tangential wall and the most conspicuous and mechanically effective layer.

In each case the bulk of the seed is occupied by perisperm which is chiefly starch. The cells are as a rule elongated in a radial direction and very narrow. A layer of cells containing tannin separates them from the true endosperm which is aleurone. Whether the intermediate tannin layer occurs before absorption/

absorption of food reserve takes place, was not investigated. It is not mentioned by HUMPHREY for *Costus* and *Amomum*, the only seeds which apparently he studied in detail for this family.

Germination - is of the pronounced ligulate type described for *Canna*. As in the latter, it is almost impossible in some cases to determine the structure of the primary root which may indeed be absent as an individual root although its axis is laid down, e.g. *Brachychilium*, or may function only for a few days as in *Hedychium*, *Alpinia*. The growth of adventitious roots in all cases commences after a few days. The plumule is remarkably well differentiated on germination and breaks through the ligule of the cotyledon before the plant is a week old, e.g. in *Brachychilium Horsfieldii* (Fig. 94). The massive character of the plumule dominates the seedling: the third leaf has its rudiments forming in a seedling two days old, at which stage the radicle is represented by the blunt basal end of the embryonic plant which has emerged. Buds are found in the axils of leaves in seedlings one or two weeks old.

The sheathing base of the cotyledon is reduced in each almost to extinction. In all but *Amomum*, the/

the stalk connecting suctorial tip to sheath and ligule is absent or almost so. Thus the cotyledon may be regarded as consisting almost entirely of suctorial tip and ligule, developed to an equal extent. The former is extremely efficient, it is cylindrical or spindle-shaped, as in *Canna*.

The anatomy of seedlings of different genera will now be considered, individually.

Tribe I. Hedychieae.

HEDYCHIUM

Hedychium Gardnerianum.

Seven seedlings were sectioned.

Anatomy of one-week-old seedling (Fig. 85).

At this stage the first leaf had just pierced the apex of the cotyledon ligule.

Cotyledon. Two vascular strands lying diametrically opposite proceed from the tip, horizontally through the short stalk and diverge.

Strand (a), the upper, enters the ligule, turns vertically upwards, bends very sharply when half way up, (so that it appears in transverse section as one strand) descends vertically but now is on the side adjacent to the axis, (giving the appearance of two strands/

strands in transverse section). The downward trace turns inwards at a level above the stalk, fusing with a xylem group derived chiefly from the mid-rib of the first leaf.

Strand (b) does not enter the ligule: it continues in a horizontal direction entering the axis at the base of the first node which is placed on a level with the stalk and seed. There it divides. One half ascends the first internode maintaining a lateral position, on the side nearest the seed, its trace becomes weaker and finally merges into the plumular meristem. The other half of strand (b) fuses with the strands of the plumular axis, without departing from its horizontal course.

The first leaf, at this stage, is provided with a mid-rib and two pairs of strong lateral strands. The ring of five strands which are therefore found at its base are reinforced in the first instance by strand (a) on completion of its course and, almost immediately, by that half of strand (b) which does not run upwards through the internode, independently.

Below the cotyledon stalk (and, since the cotyledon strands have now lost their entity, in what may be therefore looked upon as hypocotyl) the strands become resolved into four bulky groups. That which is/

is nearest the cotyledon stalk is comprised of most of strand (b) plus the outer laterals of the first leaf. The vertically opposite group consists chiefly of strand (a). Lower, a symmetrical pattern of four quadrants divided by parenchyma, results. Each quadrant is cut off from the parenchyma by xylem which surrounds the phloem on two sides. Rotation and fusion follow, giving a tetrarch root.

Longitudinal sections confirm the above observations.

Anatomy of two-days-old seedling.

At this stage the axis of the seedling was curved and ligular development had not commenced. The anatomy is exceedingly simple. As in the later stage, two strands leave the cotyledon tip. Outside the seed, in the uppermost part of the sheath which will ultimately produce the ligule one strand divides in two but the halves reunite above the plumular bud: only three traces are differentiated in the first leaf, and the combined cotyledonary and plumular traces amount to four. A scattered arrangement prevails in the hypocotyl. The primary root is tetrarch. It is thus seen that the only indication (if it is so) of a future ligule supplied with vascular tissue, is to/

to be found in the apparently futile splitting and subsequent fusion of the elements of one of the cotyledonary traces.

Morphology of the first leaves. If RENDLES' nomenclature for the parts of the adult Zingiberaceous leaf be taken, i.e. if it be divided into "sheath, stalk and blade with a ligular outgrowth of the sheath", then the following sequence arises.

The first leaf is entirely sheath and completely enrols the younger leaves. It is linear, with a rounded hood-like apex (Fig. 86). The veins are parallel and consist of a mid-rib and two pairs of subsidiary strands, which are supplemented by another pair as the girth of the seedling increases.

The second leaf is in the main a sheath. Towards the upper limit there is a deep constriction, beyond which there is a small leaf-like tongue. The veins run uninterruptedly to the tip. There is a foreshadowing of the adult form; the two flaps of tissue below the constriction, although not the wings of the ligule, at any rate suggest them.

The third leaf, the blade of which is convolute in the bud, attains the adult form. The sheath has the appearance and length of the first leaf. At its upper limit the hood-like ligule which completely covers the sharp tip of the fourth leaf, is found projecting./

projecting. The blade is obovate lanceolate. When the sheath is flattened out it is seen that the ligule is formed of two wing-like projections of the margins of the sheath, which overlap and coil one on another in the normal position. The veins are parallel in the sheath, converge at the constriction between sheath and blade (where a stalk occurs in leaves possessing such), bend out towards the margins of the blade and converge again at the sharply pointed tip.

Hedychium coccineum carneum - presented no new features. The testa is black and not reddish-brown as in *H. Gardnerianum* and the third and succeeding leaves had a short stalk.

Hedychium spicatum var. acuminatum. Three seedlings were examined. The leaf in its adult form, as shown by the third leaf, had a stalk between blade and ligule.

ROSCOEIA

Roscoea purpurea.

SARGANT and ARBUR (107) who describe the cotyledon as having an upper (i.e. a ligular) but no lower sheath, state that there are two strands in the cotyledon/

cotyledon and that root-plates and cauline roots are found above the first node. They refer to the cotyledon anatomy as being similar to that of *Elettaria*, in which both cotyledon strands enter the sheath (i.e. "ligule" - L.B.) following an asymmetrical course. The species below have only one cotyledon strand in the ligule.

Roscoea cautleoides. Two seedlings were examined.

Cotyledon. Two strands proceed from the tip but only one enters the ligule. It ascends to the apex and runs down to the base of the sheath which is in length approximately one-third of the ligule.

The two cotyledon strands join the plumular traces at the base of the first node which is long. The mid-rib of the first leaf remains independent for some distance after the two pairs of laterals and the second leaf traces have formed a central mass. The xylem in the upper part of the hypocotyl is scattered; lower, it moves to the centre and, at the base, forms a diarch root stele.

BERRIDGE (9) has observed mesarch bundles in the cotyledon tip but has decided against their having a phylogenetic value. (See Final Summary).

Roscoea/

Roscoea alpina and R. Humeana - have similar structure: serial sections of these were not taken.

BRACHYCHILIUM HORSFIELDII

SARGANT and ARBER describe the anatomy of the transition.

Cotyledon - has two strands. The tip is inserted "partly on the sheath, partly on the axis", (although the region below the cotyledon cannot be described adequately as "axis" and the expression "ligule" was evidently used subsequent to this paper, for the upper "sheath"). The strands may not enter the ligule.

The hypocotyl has an arrangement of three plumular and two cotyledon strands. The structure of the primary root was not determined.

In the present study only longitudinal microtome sections and hand sections, cut transversely, were made.

Tannin was found in the cells of the leaf in this and other genera.

Tribe/

Tribe III. Zingibereae.

ALPINIA CALCARATA

Germination and Seedling - as in Hedychium.

SARGANT and ARBUR note that the first leaf is preceded by a ^{sheath} ~~seale~~. Actually, as in Brachychilium, Hedychium etc., the mature type of leaf is not apparent in either the first leaf (the ^{sheath} "scale" referred to) or the second. Further it is taken for granted that because two strands proceed from the cotyledon tip and the plumule provides three endarch bundles that the hypocotylar anatomy will be the same as for Brachychilium, but this and the root structure were not determined by SARGANT and ARBUR.

The rather unusual anatomical features found in seedlings of Alpinia recall the structure of Hedychium.

Anatomy. If the ligule of the cotyledon be peeled off, flattened out and examined, it is seen to be free of vascular tissue, or in a few cases a single vascular strand curves upwards for a very short distance at the base of the ligule.

Transverse sections (Fig. 97) examined from the root upwards show a tetrarch root stele, gradually assuming a more scattered appearance as the short cotyledon stalk is reached. Two strands proceed from/

from the tip of the cotyledon, through the stalk, but instead of one or both turning downwards towards the root, by a direct or indirect course both strands turn upwards. The first node is oblique.

Strand (a) approaches the central mass of vascular tissue immediately below the point where the first internode begins. It splits into three strands; the median one moves in to the core of the axial strands, the lateral portions remain peripheral. At this level the second cotyledon strand (b) also enters the plumular axis. Its behaviour is similar to that of strand (a).

Four of the five strands of the first leaf are derived solely from the cotyledonary traces, which provide one-third of their total number of elements for the supply of second and succeeding leaves. The direct contribution of the cotyledon strands is nil, and this is the first instance yet encountered where it can be truly stated that there is no sheathing base provided by the cotyledon.

SARGANT (107) describes the seedling of *Amomum* and *Elettaria*.

B. SUB-FAMILY COSTOIDEAE

COSTUS SPECIOSUS

An account of the germination and seedling of this/

this plant has already been published (16). Its chief interest lies not only in its wide divergence from the Zingiberoideae, both in external and internal morphology, but in the occurrence of a ligule similar to that of the adult leaf at the base of the cotyledon lamina. At the apex of the lamina where the cotyledon tip enters the micropyle of the seed, there arises a small spherical outgrowth, devoid of vascular tissue. Several tentative suggestions were put forward to account for the occurrence of these two structures.

The cotyledon tip is a narrow cylinder; the blade is a wide flattened structure with highly differentiated tissues even in a seedling a few days old. Five strands proceed through the lamina. In the hypocotyl the cotyledon and plumular traces behave independently of one another. No fusion between them occurs until the base of the lengthy hypocotyl is reached, at which level cauline roots arise profusely. The primary root ~~never~~ functions. The internal structure of a three-months-old seedling gives an indication of the vitality and rapid progress of the seedling.

The external morphology of *Costus spicatus* is similar to that of *C. speciosus*. The internal structure/

structure has not yet been investigated.

LITERATURE ON THE SEEDLINGS OF THE SCITAMINEAE

Cannaceae. The work of HEGELMAIER, SCHLICKUM, HUMPHREY and GATIN has already been noted. HUMPHREY remarks that HEGELMAIER'S observations on the rupture of the testa at germination are faulty. LUBBOCK gives a short description of a typical germination of this family.

Marantaceae. LUBBOCK'S account of this family ends at a short discussion of the dehiscence of the fruit. HUMPHREY refers merely to the curved embryo of *Thalia*. Information with regard to the initial stages in the life history of members of this family is therefore almost entirely lacking.

Musaceae. HUMPHREY deals with the embryo and seed of *Musa*, *Strelitzia* in which there is no functional perisperm, and *Heliconia* which has no micropylar collar. GATIN gives a very full account of the embryo and germination of *Ravenala*, *Strelitzia*, *Musa* and *Heliconia*. The latter is abnormal in the very poor differentiation of the embryo. The cotyledon of *Musa*, in the embryo, has a somewhat unusual form.

GATIN/

GATIN in a survey of the germination of Cannaceae and Musaceae, which in every case is ligulate, draws certain conclusions, a few of which will be summarised:-

- i. The external morphology of germination is in accordance with the curvature of the axis of the embryonic plant as in the Palms.
- ii. Heliconia is exceptional in its poor differentiation in the embryo and the differentiation of the central cylinder before the radicle, as in Palms.
- iii. Germination consists of two phases as in Palms.
- iv. The endogenous nature of the radicle in the embryo is emphasised. If the embryos of the series
Gramineae - Palmae - Musaceae - Alismaceae
be considered, the most deep seated radicle is in the grasses, it is less so in the Musaceae and in Alisma is the continuation of the general epidermis of the embryo.
- v. Since the strands of the cotyledon form at its base an arc of a circle which may have a plane of symmetry through a median bundle or through two groups of identical bundles this group cannot furnish evidence for SARGANT'S double bundle theory.

Zingiberaceae. The researches of HUMPHREY on the seed and embryo, and of SARGANT and ARBUR on certain seedlings, have been mentioned. BERRIDGE found mesarch structure in certain vascular strands in the tip of the cotyledon of *Brachytilium Horsfieldii*, but concluded that they had no phylogenetic significance.

AMARYLLIDACEAE

Seedlings of *Alstromeria* sp. were examined (Fig.).
 The anatomy of the transition has already been described by SARGANT (193). There are two strands in the cotyledon and the primary root is diarch.
 Growth, once begun, is very rapid.

COMMELINACEAE

Members of this family may be either annual or perennial. Seedlings of plants of the former group should not legitimately be described with plants having rhizomes, but in the Commelinaceae the germination and seedling structure are so uniform that the habit of the plant seems in no way to affect it. A description of a type will serve for all the species examined.

TINANTIA FUGAX

Seed - varies in shape according to its position in the capsule and the number of seeds present in it. It is generally roundish or cubical, diameter approximately 2.5 mm. and is covered by a black leathery, warty testa. A small circular lid is developed at a point opposite the radicle. It is pushed out on germination. The abundant endosperm is starchy.

Germination/

Germination is hypogeal. The cotyledon which is non-ligulate consists of a long sheathing base connected to the suctorial tip by a slender thread-like stalk the length of which seems to depend on the depth of the seed in the soil, since it elongates, keeping pace with the growth of the sheath while the somewhat heavy seed remains at its original level. The first leaf emerges by rupturing a line of weakness in the apical part of the cotyledon sheath (Fig. 106).

Growth is rapid, the first leaf appears above ground during the first week and is followed by a succession of four or five leaves before the seedling is six weeks old.

Primary Root - is well developed in the seedling two or three days old; it is soon surrounded by four strong adventitious roots arising from the base of the hypocotyl equidistant from each other. A further set of four are produced later, alternating with the first set and immediately above it.

Hypocotyl. This is difficult to distinguish in the first few days after germination. In a week it is discernible as a cylindrical, smooth, semi-transparent structure, at the upper limit widening where the cotyledon sheath and first node arise, at the lower/

lower limit constricted very abruptly. The hypocotyl continues to increase in length at the same pace as the stalk of the cotyledon. Its length may be equal to that of the cotyledon sheath.

First leaf - is obovate to lanceolate in shape, with a sharp apex, and is very thin. When fully expanded the blade is 2 cm. long and 1.5 cm. at its maximum width. It has a mid-rib and two to four pairs of lateral strands, the number depending on its age. Multicellular hairs arise obliquely on the margins and upper surface of the blade. They consist of two or more cells of which the terminal ends in a very sharp point, like a spine (Fig. 107).

Anatomy. Two strands run parallel through the stalk of the cotyledon. In the sheath one, immediately on entering it, descends to the base. The other may ascend for a short distance and descends on the opposite side of the sheath. At the base of the cotyledon both strands become oblique and tend to converge towards the centre. They do not fuse but continue their course in a central position to the base of the hypocotyl appearing as two wedge-shaped traces in transverse section.

At the base of the first node the mid-rib dichotomises. Two strands in the hypocotyl are therefore provided/

provided by it. The lateral strands of the first leaf first fuse in pairs, which themselves unite at the upper limit of the hypocotyl only to divide again into two traces. The second pair of plumular traces have their origin in the subsidiary strands of the first leaf. The four plumular traces are disposed like the corners of a square about the cotyledon traces.

The tetrarch root stele at the base of the hypocotyl seems to be formed entirely from the cotyledon strands. Each plumular strand is in direct continuity with an adventitious root. The internal structure thus accounts for the regularity with which these roots arise. Since the plumular strands have no connection with the primary root, the need for such a ring of roots is apparent. It is also clear that the primary root is under no necessity to increase in length or girth since the growth of the plumule makes no demands upon it.

It is worthy of note that this arrangement, whereby the first leaf is provided for in a manner independent of the radicle, is already made in the ripe embryo (Fig. 106) in which the presence of the meristem for the four adventitious roots is very marked.

The lowest internode in a six-weeks-old seedling (Fig./

(Fig. 106) is still surrounded by the cotyledon sheath. The stem anatomy is typical, there being ten central closed bundles, and sixteen in the periphery. They fuse together with the cotyledon bundles; a swollen region indicates this level. In the thick hypocotyl there are four strong vascular strands. Four lateral roots emerge at the upper limit of the hypocotyl. Four root initials alternate with them.

The rapid development indicates that the plant is an annual. Seedlings of *Commelina coelestis*, *C. dianthifolia*, *C. graminifolia*, *Cyanotis cristata*, *Rheo discolor*, and *Tradescantia geniculata* var. *Kunthiana* (Fig. 109), were also sectioned. There was, in general, uniformity in the anatomy except for the radicle of *Cyanotis* and *Tradescantia*, both of which had triarch steles. Multicellular hairs covered the upper surface and margins of cotyledon and leaves of *Tradescantia*, while the cells ^{of} the abaxial epidermis of cotyledon and leaves of *Cyanotis* and the three species of *Commelina* were markedly papillose. It was observed that chlorophyll did not develop in the *Commelinas* until the end of four or five weeks.

LITERATURE ON SEEDLINGS OF COMMELINACEAE

HOLM/

HOLM (71) gives a brief account of the seedling of *Commelina nudiflora* without fully describing the anatomy. MARTHA HOLLINSHEAD published detailed notes on the germination of *C. communis* L. The anatomy of the hypocotyl is, however, omitted.

The early work of SOLMS-LAUBACH (116) on the embryo and his discovery that the plumular bud was terminal gave rise to much speculation, since the terminal nature of the cotyledon was one of the most serious difficulties in deciding its homology.

I R I D A C E A E

DIPLARRHENA MORAEA

Seed - small, flattened.

Germination - Type V. with a cylindrical green cotyledon, tapering to the tip and sheathing at the base. The seedling and its anatomy present no peculiar features. The first leaf has a mid-rib and four subsidiary strands, there is a single cotyledonary strand, and the primary root is tetrarch at the upper limit, becomes triarch and is finally diarch at the tip.

LIBERTIA/

LIBERTIALibertia grandiflora.

Seed - pear-shaped; the testa is brown.

Germination - Type V. with a subterranean cotyledon.

A slender stalk connects tip and base. The sheath is open after the first leaves develop. There is a single strand in the cotyledon. Three traces from the plumule fuse with it to give a diarch root.

Libertia ixioides - differs from *L. grandiflora* in having a very long thin stalk leading to the cotyledon tip.

MARICA HUMILIS (= M. gracilis)

Seed - 4 mm. long, flattened on two sides, curved on the third; testa brown.

Germination and Seedling - as for *Libertia*. The copious production of root hairs and, later, of lateral roots, and the lengthy first node are noteworthy.

Anatomy. There is one strand in the tip of the cotyledon, but three in the sheathing base. An endodermal sheath is laid down extending half round the central cylinder before the cotyledonary traces enter it. The root stele is polyarch and in the older seedlings/

seedlings becomes markedly schlerose.

IRIS

The following species provided material for examination -

Iris germanica	Iris Pseudacorus
" italica	" stolonifera
" Nertchinskia	" Swertii

Germination - as for *Libertia*. There is some variety, however, in the nature of the cotyledon. RENDLE (96) remarks that three of KLEBS' types are represented; *Iris Pseudacorus* (Fig. /) conforms to the type with sword-shaped cotyledon sheath; *I. sibirica* "affords instances of the second type which is the more general one in the order, showing a more complete differentiation of the cotyledon into a sheathing base and an absorbent tip, the two parts being connected by a slender portion. The third or epigeal type, where the cotyledon forms the slender tapering first green leaf has been described in a species of *Iris*".

As has been suggested already, there is no essential difference between these types, of which the third has not been encountered.

The length of the sheath varies from two to five mm. in length. The connecting stalk may be very short/

short or exceedingly long, but the germination of *I. germanica* shows that no significance can be attached to this. The length of the stalk depends on that of the hypocotyl. The germination of *I. germanica* was viviparous, the elongation of the hypocotyl being a means of propelling the seedling between the neighbouring seeds and through the capsule, so that the plumular bud is free to develop. Another result of vivipary is seen in seedlings the plumule of which does not emerge after the radicle, but develops inside the seed coat, piercing it at the end remote from the micropyle.

In one instance, viz. that of *Iris ensata* var. *Pabularia* a cotyledon with a ligule was produced. If it is possible, further sowings will be made of seed of this species, from the original and a new source, in order to confirm this observation.

Anatomy. The cotyledon in each case has either a double bundle, a single bundle or a single bundle which becomes double at the base of the cotyledon. The primary root may be diarch, triarch or tetrarch. The number of strands in the first leaf is variable, seven or nine strands are commonly found.

SISYRINCHIUM

Three species, viz. *S. californicum*, *S. pachyrhizum* and *S. striatum* provided material for investigation. In each species the long filiform cotyledon has a double bundle and a diarch root. There are three strands in the first leaf which is ensiform. Germination for the three is epigeal. The primary root is lengthy and persistent.

The uniformity in germination and anatomy of the seedling is noteworthy in view of the statement of HOLMS that "it would be interesting to know whether the species of (BENTHAM and HOOKER'S) three sections (of *Sisyrinchium*) germinate in the same way". HOLMS found a striking similarity in the anatomy of the adult for the genus, in general, this research having been suggested by the tendency at the time (1908) for some American writers to raise these sections, *Bermudiana*, *Echthronema* and *Eriphilema* to generic rank, a procedure which HOLMS from his anatomical studies considered unjustifiable.

No species in the first section had its seedling anatomy investigated; *S. striatum* and *S. pachyrhizum* in the second section are indistinguishable from *S. californicum* in the third. The three species agree in external morphology with *S. angustifolium*, described by/

by HOLMS. Unfortunately he adds no anatomical data.

ARISTEA ECKLONII

The adult plant is of the erect herbaceous type with a root stock short, thick and oblique (5), and belongs to a genus containing two of the four shrubby Iridaceae, viz. *A. corymbosa* and *A. fruticosa* (112). No indication of such a relationship is afforded by the seedling.

Germination is of the type seen in *Tigridia Pavonia*, with a sharp angle between the stalk of the cotyledon and the sheathing base. The seedling differs in no way from those of the majority of the family. It is as simple anatomically, the primary root being diarch, although triarch at its upper limit, while there is a single cotyledonary strand, which does not extend an appreciable distance into the upper sheath. The first leaf has a mid-rib and two lateral strands.

DISCUSSION

- (a) The grouping is in several respects unsatisfactory since the term rhizome is applied to such widely differing organs as ^{the} thin creeping underground stem of some species of *Trillium*, and the bulky perennating bodies of ~~many~~ of the garden varieties of *Iris*. Further, the/

the growth may be monopodial or sympodial, although the seedling stages do not reveal which it may be. In many instances the rhizome does not develop until the plant is far beyond the seedling stage. Thus there is no apparent difference in the seedling of an annual or perennial Commelinaceous plant: only the more rapid growth of the former would suggest the habit. It was scarcely to be expected that this group would show the same uniformity found in others, for example the bulbous group, in which the perennating organ varied little, or not at all, in its form.

- (b) On this account, doubtless, family resemblances are strongly marked. The Zingiberaceae and Commelinaceae for instance, form complete units apart from considerations of habit.
- (c) Germination is hypogeal with a ligulate cotyledon in Zingiberaceae and Cannaceae. Epigeal and hypogeal germination and cotyledons with or without ligules are found in Iridaceae and Liliaceae. Seedlings of plants belonging to the same tribe tend to have the same type of germination and cotyledon, Medeolae and Hemerocalleae in the Liliaceae furnish examples of this.

In/

In Liliaceae the hypogeal ligulate cotyledon predominates as far as the seedlings examined are concerned. The Iridaceae have in almost every instance a non-ligulate cotyledon which as a rule is subterranean.

- (d) Plumular development is strong and growth of the early leaves rapid, in the hypogeal type of seedling. The importance of the plumule is indicated by its differentiation in the embryo. Heliconia in the Musaceae is conspicuous by the retardation in plumular development whereas Canna is remarkable for the advanced condition of the plumule in the embryo.
- (e) The radicle is variable in its development. In Cannaceae it is missing, as a morphological unit, although its vascular tissue is differentiated in the embryo. The radicle in Commelinaceae is ephemeral being replaced by cauline roots, which originate with beautiful symmetry and precision. The Zingiberaceae dispense with the primary root after a week or so, and in some genera the radicle, as in Canna, is lacking as an organ; the need for the copious supply of adventitious roots is obvious. In all the foregoing families with early adventitious/

adventitious roots, the initials of these are apparent in the embryo.

(f) Cotyledon anatomy provides a few interesting features.

- i. In Liliaceae the double bundle or its equivalent is the common vascular system. The *Medeolae* are exceptional in the laminate nature of the cotyledon and in having a midrib and two lateral strands in the stalk and base of the cotyledon, possibly in relation to the long life of the cotyledon and its value as the only photosynthetic organ for a season. The cotyledon of *Hemerocallis* has strands varying in number from four to seven. The number is not constant even in a species.
- ii. In Iridaceae the cotyledon possesses a double bundle, or a single bundle becoming double towards the base, or a single bundle.
- iii. The cotyledon of seedlings of Commelinaceae has two strands following a parallel course throughout the greater part of the cotyledon.
- iv. The Zingiberoideae have two strands in the cotyledon, but their behaviour is by no means uniform.
 - (α) Both strands may enter the ligule as in *Roscoeae*, though one may do so only for a very short distance. The strand which ascends to the top of the ligule then helps to stiffen the ligule (as SARGANT and ARBUR have pointed out).
 - (β) One strand may descend to the base of the cotyledon while the other ascends the plumular axis as in *Hedychium*.
 - (γ) The ligule may be without vascular tissue, the two cotyledon strands fusing with the plumular strands in the hypocotyl as SARGANT and ARBUR record of *Brachychilium*.

- (δ) Both strands may enter the plumular axis and connect directly with the plumular bud. The primary axis is then supplied with plumular and all the cotyledonary vascular tissue. This arrangement is found in *Alpinia* and recalls SCHLICKUM'S findings for *Zizania aquatica*. His figure () is reproduced for purposes of comparison.

The large number of strands in *Costus* (*Costoideae*) affords a marked contrast to the constancy of the two strands in the other sub-family.

- iv. The *Cannaceae* may have from five to seven strands in the cotyledon sheath. The sheath is taken as the most satisfactory region for comparison since the numbers in the cotyledon tip assume such large proportions and, being mere ramifications, such numbers can have little significance.

(g) Root anatomy on the whole is simple.

- i. Two, three or four protoxylem groups are common in *Liliaceae*. *Hemerocallis* with a pentarch, hexarch or heptarch root is again exceptional.
- ii. The stele in the radicle of *Iridaceae* varies from diarchy to tetrarchy.
- iii. Tetrarchy or triarchy is the general rule in *Commelinaceae*.
- iv. The *Cannaceae* have no primary root stele of such a nature as to be determinable.
- v. Diarch and tetrarch roots are found in *Zingiberoideae*. The pentarch or hexarch root of *Costus* is in accordance with the anatomy of the cotyledon.

- (h) A distinct hypocotylar region is rare save in the *Commelinaceae* in which the hypocotylar development is/

is pronounced, and in several members of the Liliaceae, e.g. *Chlorophytum*, the hypocotyl of which has root structure. The hypocotyl is absent whenever the cotyledon is ligulate. The swollen nature of the hypocotyl in the *Medeolae* is reminiscent of the tuberous hypocotyls in the previous group, with a comparable vascular structure.

- (i) The first foliar organ in *Cannaceae* and *Zingiberaceae* may be a scale leaf, the mature type of leaf not appearing until the third leaf expands.
- (j) The precise germination mechanism by which a micropylar lid is pushed out by the elongating embryo, is seen in *Commelinaceae*, *Cannaceae* and certain of the *Zingiberaceae*.
- (k) There are no marked divergences in size of seed from the normal except in the case of the *Cannas* and species of *Hemerocallis*. The exceptional nature of the cotyledon and root anatomy is recalled in this connection.
- (l) The fact that *Bowiea* and *Chlorophytum* are placed in the same tribe of *Liliaceae* while differing in the habit of the adult and presenting two different types of germination and of cotyledon, is worthy of note.

PLANTS SHOWING THE CLIMBING HABITA. NON-WOODY TYPEGLORIOSA SP.

Seven seedlings examined.

Seed. Single seed lies in the berry which is the fruit and is 6.0 mm. in diameter. Filled with extremely hard endosperm (not starchy) in which the embryo, a straight thread-like body, 2 mm. long, lies. Never above soil level.

Germination. The primary root emerges and elongates immediately. When it is 10 mm. long the plumule will be found just outside the seed coat. The bulk of cotyledon still remains within. At this early stage, the first leaf will be distinct and well differentiated. A ligule is thrown up, and plumule breaks through.

Cotyledon. By no means dominant in the early stages. Function mainly suctorial. Hence -

- (a) Well developed club-shaped suctorial tip, constricted where it leaves the seed.
- (b) A very short stout stalk ($\frac{1}{2}$ mm.)
- (c) A "ligular" portion, the dominant part of seedling at every stage, re length. It keeps pace with elongating/

elongating first leaf (3 mm. - 10 mm. long), and is provided with a slit for emergence of plumule of the first leaf.

(d) A short but fleshy sheathing base ($1\frac{1}{2}$ mm. long).

Plumule. Well developed; massive in comparison with seedling as a whole. The first leaf is well supplied with vascular strands, having a mid-rib and four pairs of laterals.

Hypocotyl - almost non-existent.

Primary Root. Its importance emphasised from beginning and maintained throughout development. Its growth in width and length is remarkable. In a plant a few days old in which the first leaf is 2.5 mm. long and enclosed in the ligule and base of cotyledon, the root is 10 mm. long. It presents a succulent transparent appearance. A piliferous layer appears to be absent for the epidermis is smooth throughout the whole length of the root. By the time the first leaf is free, at which time it is approximately 7 mm. high, the root has begun to throw out numerous laterals at right angles to the stele, though none break through the epidermis of root. The first adventitious root is then making its way through the cortex at soil level.

Anatomy/

Anatomy. This is variable, so four types will be described.

- (a) Four well defined strands pass in pairs through suctorial tip. Below stalk, two double bundles pass into sheath and join the plumular meristem at slightly different levels. The plumular meristem consists of three masses which later resolve into two. After union with cotyledon strands there are six xylem traces which by union of a pair, become five; these arrange themselves in two crescents (each formed from a pair) joined by the fifth. The proto-xylem moves outwards. Splitting of fifth uniting xylem band into two more peripheral strips results in a hollow rectangular patch of xylem. This gives a diarch root (Fig. 122).
- (b) The course of strands in the tip unknown. Three strands run through from cotyledon stalk. The central one proceeds vertically for a short distance then bends sharply downwards through the sheath. The laterals proceed to the top of ligule and turn vertically downwards in a course parallel and very close to the upward one (giving the appearance of double bundles). At the bottom of the ligule each is evidently reinforced by a supply/

supply from tip, for below the stalk they present a double appearance. The central strand is single. One lateral fuses with the plumular meristem (derived from five first leaf bundles). Lower the central and second lateral do the same. Three separate xylem rays result. These unite, the protoxylem moves outwards and a triarch root results (Fig. 120).

- (c) Two lateral strands proceed from cotyledon stalk, close together, ascend the ligule at the top of which they separate and proceed to the base of cotyledon, one entering stele before the other. They remain single throughout; not strengthened at any point. The middle strand leaves seed but does not enter ligule; it is single, and proceeds downwards through 230 and enters stele after the first lateral and with the second lateral. Triarch Root (Fig. 123).

- (d) Compromise between (b) and (c). Central strand double; one lateral double below stalk (i.e. reinforced at level of stalk). Other lateral single (Fig.). Root almost 4-arch (actually 3-arch with isolated element representing fourth arm of xylem. (Fig.).)

Further development of the seedling.

The seedling of a month old has increased in girth in the region of the cotyledon sheath and upper part of the root. Further the cotyledon sheath is deeply slit and a longitudinal rupture has been made in the epidermis of the root. Sections taken below the constriction which in young seedlings marked the upper limit of the root, show that the root epidermis no longer protects cortex and stele of a root but the base of the first and second leaves and the plumular bud. The beginning of the stele of the primary root is to be found two or three mm. lower than its original level. Further, the primary root, which has a semi-transparent epidermis and cortex, now appears to be traversed by three steles instead of one. The epidermis is very loose; when peeled off or when sections of the root system are made, it is seen that two adventitious roots have arisen at the base of the stem. Instead of making their way outwards, they have grown in a direction parallel to the central cylinder of the radicle and through the cortex of the radicle, the cortical cells as they do so becoming disintegrated in their neighbourhood. Each behaves independently of the other, and of the primary root stele, which, towards its tip, gives off numerous/

numerous lateral strands in a horizontal direction. The adventitious roots have six poles, peripherally arranged in the stele. The explanation of the change of position of the radicle seems to be that the adventitious roots act as pull roots, dragging the plumular axis downwards through a hollow cylinder, formed by the breaking down of the cortex of the radicle. The exact manner in which the vascular cylinder of the radicle accommodates itself to this change, or what share it has in pulling down the plumular axis, has not been yet investigated.

It was found on consulting the literature on *Gloriosa* that QUEVA (94) has given an account of the phenomenon just described as well as the anatomy of a seedling of the (a) type.

The tuber of *Gloriosa*.

QUEVA writes in great detail of the production of the tuber. The preparation for tuber formation is made in the seedling at the age of that described, viz. one month old.

Young plants of eight months old were examined in the present study. Three or four aerial leaves had expanded: they had no tendril on the tip. By this time the sheath provided for the root system by the radicle had sloughed off. The remains of it still/

still adhered to the lower part of the roots which arose from a pear-shaped tuberous body. This body was subterranean. It was covered by two thin leaf bases, which, when removed, were seen to have nine vascular strands. They were the bases of the first and second foliage leaves. The naked tuber, from the top of which arose the base of the third leaf, was smooth but had a marked ridge, running from the base of the tuber to the apex. Sections through the tuber showed that it possessed stem structure. Strands were arranged peripherally and also centrally. In addition a solitary strand, which had given the appearance of the ridge referred to, ran independently in a marginal position. It is the principal strand of the third leaf.

The tuber is the result of accumulation of starch on the part of the lower half of the third internode. Hypocotyl and the first two internodes take no part in its formation, though the bases of the first and second leaves provide a tunic for it. The bud in the axil of the first leaf aborts. Those in the axil of the second and third leaves are replaced by meristematic patches, on the dorsal and ventral sides of the tuber respectively. They are the growing points by the activities of which extension of the tuber/

tuber occurs. One, the "búd" of the second leaf axil, occurs towards the base of the tuber: the other is placed half way between the apex and base. QUEVA believes that although no trace of tuberosity is apparent in the embryo, the seedling has a structure with several significant features e.g. the long sheath of the first two leaves, the shortness of the first two internodes, lack of buds in the axil of the cotyledon and the first two leaves, and the "axillary canal" which prolongs the axil of the third leaf to within a short distance from the second node. In the present investigation, longitudinal sections were not made of sufficiently old seedlings to show this axillary canal.

The characteristics of the plant, indicating the climbing habit will be included in the discussion on the group.

B. WOODY TYPE

The two genera examined are both Liliaceous.

Tribe Luzureagae.

LAPAGERIA ROSEA

The plant is a high climbing shrub having coriaceous, heart-shaped leaves with three-five nerved reticulate venation/

venation (Fig. 124).

Seed - barrel-shaped, 4.5 mm. long; covered with a thin transparent testa. The endosperm is extremely hard.

Germination. The radicle emerges at the micropylar end with the plumular bud as a swelling a little distance above the very marked root cap. Development, once begun, is rapid.

Cotyledon - is always below the soil, It consists of:-

- i. sheath, most conspicuous in the very young seedling;
- ii. stalk, short and thick;
- iii. suctorial tip occupying half the seed, club-shaped.

Development of the shoot. From the first, the plumule is dominant. A large bud occupies the axil between the cotyledon and first leaf. A short stalk with terminal bud makes its appearance. As it elongates it is observed that the first and second leaves, or the first leaf alone, may be rudimentary. The third leaf reproduces the shape and venation of the adult plant: it has a strong mid-rib flanked by two pairs of lateral strands which fuse at the base of the lamina, so that three strands pass into the petiole.

In/

In one seedling the bud in the axil of the cotyledon has emerged from the cotyledon sheath (Fig. 125).

Primary Root, strong and persistent; it tapers towards the tip. Its length increases at the same pace as the shoot in the initial stages. There is a very effective root cap (Fig. 125).

Anatomy.

Cotyledon. Three strands, the central being a double bundle, run through the cotyledon tip and stalk, placed equidistantly.

Primary Root - has seven or eight poles; there is an obvious contribution from the plumular bud to the root. The bud in the axil of the cotyledon is supplied with a strong vascular strand passing to the root. There is a very short hypocotyl, having stem structure (Fig. 124).

The climbing habit is indicated in the anatomy of the stem in which the xylem vessels are very large and there is a good proportion of phloem, the bundles being bicollateral. They are arranged in the Dicotyledonous manner, an inner ring of large strands and an outer ring of small ones (Fig. —). At the base of the stem, the cotyledon traces are inserted on those of the plumule to form a closed woody ring, with phloem to the outside and a large pith/

pith inside. A little lower down this ring breaks up to give the seven or eight poles, with phloem alternating. The woody nature of the plant is therefore revealed at a very early stage in its life history.

No literature whatever exists on the seedling and only one reference could be found relating to the adult plant.

Tribe Asparageae

ASPARAGUS

With the exception of *Asparagus racemosa* and *A. madagascariensis* all the species of which seedlings were obtained had already been described, as far as germination and embryonic structure were concerned, by EVANS.⁽³⁹⁾

A. racemosa. The embryo is similar to those of other *Asparagus* species, i.e. long, cylindrical and narrow, lying in extremely hard endosperm. It consists chiefly of cotyledon: its anatomy was not investigated. A seedling a few days old was sectioned longitudinally. The plumular bud is placed laterally in a hollow scooped out of the cotyledon. As in *Lapageria* the root is short and thick and protected by a root cap which is very noticeable. The radicle emerges/

emerges by pushing out a micropylar lid.

The plumular bud is protected at first by the overlapping margins of the slit in the cotyledon. When it emerges through the slit it consists of leaf primordia and a stem apex. The first leaf, a kataphyll, remains partially enclosed by the cotyledon sheath which is short and wide. According to EVANS the first internode never elongates and in two species the same observation applies to the first and second internodes. In such cases as the latter, the second leaf is also a kataphyll within the cotyledon sheath, and each kataphyll subtends a large rhizome bud.

In *A. racemosa* the second and succeeding internodes are long and the early leaves mere scales. The primary root increases in girth and becomes contractile. At the end of the first month a cauline root, also contractile, and three or four which are not contractile, supplement the primary root.

Anatomy. The primary root was hexarch. The stem above the kataphyll shows an arrangement of six strong vascular strands in a ring lying in a cylinder of sclerenchyma. The youngest node is traversed by three groups of strands, each group the contribution of one leaf, involving a mid-rib and a pair of weaker lateral strands.

A./

A. madagascariensis. One root of this plant had swollen to very remarkable dimensions: its stele had sixteen xylem poles, peripherally arranged. A second thin root of equal length was hexarch. It was impossible to determine which was the primary root. In all probability the hexarch root was the radicle although the swelling of the radicle of *Asparagus* seedlings to large dimensions has been recorded (39).

Anatomy of the seedling in general. EVANS found a lack of uniformity in the cotyledon anatomy of the embryo even in a species, the number of strands varying from three to five. SARGANT (103) found three strands in the cotyledon of the seedling. The primary root varies from tetrarchy to heptarchy, the extreme cases being those which have two rhizome buds within the cotyledon sheath. SARGANT notes of the hypocotyl that its traces are cotyledonary and plumular all alike and behaving in the same way during transition.

LITERATURE ON THE SEEDLINGS OF THIS GROUP.

In addition to QUEVA'S work on *Gloriosa* and the allied/

allied genus *Littonia*, only the publication by EVANS deals with the seedlings of Climbers. *Smilax*, also described by the latter author, was characterised by an undifferentiated embryo, and dominance of plumule in germination. This plumular development, it is suggested, indicates the adult habit, just as in the *Asparagus* embryo and seedling there is a dominance of stem over leaf..

SARGANT makes a brief reference to *Asparagus* in her description of Liliaceous seedlings.

DISCUSSION

While it would be inadmissable to draw many conclusions from the study of such a limited number of seedlings, certain features are constant for the group.

- (a) The primary root is remarkable for its length and the development of its central cylinder. Lateral roots are infrequent at early stages. *Gloriosa* affords a remarkable instance of augmentation of the radicle without having recourse to secondary thickening. The vascular anatomy of the root is in no way remarkable, though QUEVA lays emphasis on the fact that in *Gloriosa* the primary root stele/

stele changes from diarchy to tetrarchy in proceeding downwards.

- (b) The germination includes ligulate and non-ligulate types but in all cases is hypogeal. The only abnormality in the anatomy of the cotyledon is the variability in the behaviour of the strands of *Gloriosa*. This, like the root system, finds no parallel in the seedlings of any other species examined.
- (c) The hypocotyl does not exist as a distinct part of the seedling, but a region exists in which plumular and cotyledonary strands run parallel. Their behaviour in *Asparagus* according to SARGANT, is similar to that of hypocotylar strands in *arborescents*.
- (d) The plumule dominates the young seedling and its development is rapid. In *Gloriosa* which produces a tuber, and *Asparagus* which is rhizomatous, the first two internodes are short.
- (e) The stem structure is similar to that of a dicotyledon, doubtless because the mechanical requirements of monocotyledonous climbers are akin to those of a dicotyledon. The bundles in their nature/

nature, e.g. presence of large vessels, buttressing by sclerenchyma, bicollateral type etc. indicate to some extent the climbing habit.

- (f) The early leaves do not resemble the adult leaf. They may take the form of mere kataphylls (Asparagus and Smilax) or be very rudimentary (Lapageria). In Gloriosa the early leaves have no tendrils.
- (g) As QUEVA and EVANS have pointed out it is possible, chiefly from an examination of the plumular meristem and its development, to make some reconstruction from the very young seedling of the adult form of the plant.

PLANTS SHOWING THE ARBORESCENT
OR SHRUBBY HABIT.

L I L I A C E A E

Tribe: Dracaenae.

Cordyline Banksii

Four seedlings were examined.

Seed - 2 mm. in length, spherical or ovoid in shape.

The endosperm is absorbed rapidly.

Germination - Type V. with a cotyledon which is aerial and straightens out with the seed at its tip. A slight swelling marks the position of the plumule, development of which proceeds at the normal rate for seedlings of the family.

Cotyledon - is cylindrical, with a uniform cross section throughout most of its length. It possesses two strands with protoxylem in contact forming a double bundle.

Hypocotyl. In the young seedling this may be equal in length to the cotyledon. It has a strongly cutinised epidermis, wide cortex and a triarch or tetrarch stele with endodermal sheath. It is thicker than/

than the radicle however and externally is indistinguishable from the cotyledon sheath save that it is colourless.

Primary Root - is persistent. In old seedlings it becomes thin due to the drying and withering of the cortex, but the stele, sheathed in a very thick sclerenchymatous layer derived from the endodermis, still functions. A single cauline root assists the radicle from the first week. It is polyarch, having twelve xylem poles in some instances.

The stele of the primary root which is triarch is supplied by cotyledon and plumule. This is in agreement with SARGANT'S observations on *C. australis* which has a transition according to VAN TIEGHEM'S Type I.

ASTELIA SP.

Seed - as in *Cordyline*, ovoid, covered with a hard, polished testa.

Germination - hypogeal, ligulate. The cotyledon consists of -

- i. short sheathing base, 1-2 mm. in length;
- ii./

- ii. ligule, variable in length. It may be three or four times as long as the sheathing base, or barely as long.
- iii. Short stalk connecting with the suctorial tip which, at germination, almost fills the cavity in the seed: a mere trace of endosperm remains in the seed of a week-old plant.

Hypocotyl - comparatively short.

First leaf - as in Cordyline, is long, linear lanceolate. It has a mid-rib and a pair of lateral strands. Internodes are short.

Anatomy. The double bundle of the cotyledon proceeds from the tip to the sheath and joins the plumular traces when they have been reduced to three. Plumular and Cotyledonary strands run parallel through the hypocotyl.

Primary Root. A solid mass of xylem occupies the bulk of the stele at its upper limit; there are four phloem groups. At a slightly lower level the root stele becomes typically triarch. The primary root is long and tapering. It is persistent, but at an early stage is reinforced by a cauline root and several lateral roots. The adult plant has a short thick rhizome.

KNIPHOFIA NORTHIAE

Although the genus cannot be termed shrubby in its habit, yet it shows secondary thickening in its axis and the adult plant may have a short rhizome or short woody stem. The above species is figured as having such a stem by BAKER (/), thirty or forty leaves rising in close succession towards its apex.

Germination, as in *Astelia*.

Anatomically there is nothing of peculiar interest. There are two cotyledon strands, one of which enters the ligule, ascends to the tip and after bending sharply, descends to the base of the sheath. The hypocotyl, which is between one and two mm. in length, shows some characteristics of the root, e.g. endodermal sheath. The primary root is pentarch.

LITERATURE ON SEEDLINGS OFARBORESCENT LILIACEAE

In addition to *Cordyline australis*, SARGANT describes the anatomy of the transition for three species of *Yucca* and one of *Dracaena*. The *Yuccas* are large stout seedlings, well developed, with persistent primary roots and a first leaf which develops early: /

early: the same holds true for *Dracaena*. The cotyledon of *Yucca* may have a double bundle and two laterals (*Y. gloriosa* and *Y. aloifolia*) or six or seven strands in the cotyledon, and an additional ring of four in the wings of the sheath as in *Y. arborescens*. In *Dracaena draco* there are three double bundles and a single strand in the cotyledon while there are eighteen poles in the root stele.

KLEBS puts *Dracaena draco* into Type I., remarking on the short cotyledon sheath, while *Yucca gloriosa* belongs to Type II., i.e. the two seedlings belong to the hypogeal, non-ligulate group. CHRYSLER found that *Astelia* offered no points of significance to his study of the central cylinder though an account is given of *Yucca*. The origin of secondary thickening in this genus is discussed by SCOTT and BREBNER.

A M A R Y L L I D A C E A E

VELLOZIA ELEGANS

The plant belongs to a genus with "stems generally thick and woody surrounded by many fibrous sheaths" (96) and which is so distinctive in its habit, that, while BENTHAM and HOOKER place it among the Amaryllidaceae, ENGLER makes a family for it and the genus/

genus *Barbacenia*, mainly on floral characters. The tribe or family is made up of markedly xerophytic plants inhabiting the dry campos of Brazil, or South and tropical Africa and Madagascar. The main contribution to the knowledge of the Velloziales was made by WARMING (127). A brief account of his work is given by HOLMS (68). WARMING describes the plants as living in "stony, sunny places with but little earth for the penetration of roots", and as being perennial, with erect stems which branch dichotomously, the most characteristic feature however being "the thick coating of roots in Vellozia, which develop from the stem and proceed within the leaf sheaths towards the ground". Anatomical details are few. The leaf of *V. compacta* is composed of thin-walled transparent tissue "similar to that of the leaf of Gramineae, Juncaceae, Cyperaceae", while the adventitious roots which arise from the stem within the leaf sheaths have a "thin-walled, often starch-bearing endodermis, the central part being occupied by a heavy layer of exceedingly thick-walled stereome": an exodermis is present. WARMING makes a comparison between Vellozia and the tree ferns, *Dicksonia*, *Cyathea* and *Alsophila*. *Dicksonia* has a similar trunk, with the same internal structure: the fibrous sheath/

sheath covering the trunk in both has, according to WARMING, the same function in each. SCHULTZE, (111) writing on the anatomy of the Velloziaceae has nothing to add to WARMING'S findings. Accordingly, little is recorded of the structure of the adult plant and nothing whatever of the germination or seedling.

Seed - 1.5 mm. in length, of a flattened cylindrical shape; testa, dark brown.

Germination. The embryo is cylindrical and straight. A considerable quantity of endosperm remains at germination. The cotyledon is simple consisting of a short sheath, less than 1 mm. long, tapering to a very short stalk which terminated in a minute suctorial portion with blunt tip. Germination is hypogeal but the elongation of the hypocotyl serves to push the seed towards, and, in the greater number, a little above the surface. The first leaf makes its appearance in the first week. The primary root is long, tapering and persistent. Its upper limit is marked by a ring of long root hairs.

The general appearance of the seedling is that of delicacy. A seedling three weeks old, may be less than 5 mm. in length, measured from the root tip/

tip to the apex of the first leaf which is narrow and linear in shape. Cauline roots, often with lateral branches, are produced in the first month.

Anatomy of seedling three weeks old.

Cotyledon. A single collateral strand, having xylem and phloem more or less equally developed, proceeds from the tip of the cotyledon to the base of the sheath. The tissues of the latter show a considerable degree of differentiation. The vascular strand, which acts as a mid-rib, is protected by a strong parenchyma sheath of eight or nine large cells. Two lacunae occur, flanking the vascular strand. The adaxial epidermis consists of small regular cells; where the aerenchyma occurs; this may constitute the entire adaxial tissue. The abaxial tissue consists of spongy mesophyll, a sub-epidermal layer and the epidermis which is interrupted by numerous sunk stomata with large intercellular spaces beneath them.

The First Leaf - is provided in its early stages with a mid-rib and a pair of lateral strands: these, with the contribution from the second leaf, enter the hypocotyl as a single wedge.

Hypocotyl. The cotyledon strand passes through the hypocotyl/

hypocotyl independent of the plumular traces, which constitute the more massive bundle.

Primary Root. The diameter of the root is small, and the vascular structure of the utmost simplicity, being protostelic in nature. A central xylem core, composed of a single vessel surrounded by seven others, lies within a ring of phloem. Two sheaths are found delimiting the stele. The inner is composed of cells, thickened on all but the outer tangential wall and occupying the position of a pericycle, since they abut on the phloem. If the inner be regarded as a pericycle, then the outer sheath, consisting of large cells very regularly arranged, must be the endodermis. It has been mentioned that the roots of the adult have a thin-walled endodermis; while the outer sheath of the primary root does not show the thickened walls of the inner, its cells have slightly thicker walls than those of the cortex. There is no exodermis in the primary root at the stage examined.

The extreme reduction of vascular tissue in this seedling finds its only parallel, amongst those cases investigated in the present study, in the epiphytes and the aquatics. The similarity existing between *Vellozia* and the Bromeliads is not confined to seedling structure. The description of the habitat of *Vellozia*/

Vellozia given would have been equally appropriate for a Bromeliad, either terrestrial or a facultative epiphyte. The resemblance in habit was seen by GAUDICHAUD, who compared the aerial roots of Tillandsia and Vellozia, and DIDRICHSEN whose attention was drawn to the course of the roots in the cortex of the stem in Vellozia and different Bromeliads. WARMING considers the function of these roots to be the gathering of moisture from fogs and rains (cf. roots of epiphytes) while the fibrous sheath of roots and leaf-sheaths is a protection against excessive drought. Similarity in habit and the problems of water supply have produced a similar response in the adult.

With regard to the seedling anatomy, two views are possible. Bearing in mind the resemblance in external and internal morphology of the adult Vellozia and the tree ferns, and the protostelic condition of the root of the former, primitiveness is suggested. With a consideration of the Epiphytes and Aquatics, particularly the former, since their mode of life is exactly similar to that of Vellozia, the resemblance in anatomical detail is so striking that it is quite reasonable to regard it as an instance of environmental conditions reacting similarly/

similarly on plants of such unrelated families as Amaryllidaceae and Bromeliaceae: reduction and not primitiveness would then be the explanation.

PALMAE

The work of GATIN on the embryo and germination of the Palmae is so comprehensive, involving a description of thirty three genera and fifty eight species, that little remains to be added to it. A very brief account of the few palm seedlings dealt with in the present study will be followed by a short account of the literature on the subject, including GATIN'S conclusions from his work.

CHAMAEDOREA SARTORII

This plant was not described by GATIN.
The seed is egg-shaped, and 1 cm. in length.
Germination is of the hypogeal ligulate type. The tip of the cotyledon is spherical and is traversed by fifteen peripheral strands, composed mainly of phloem. There are four strands in the ligule and six in the sheathing base of the cotyledon. The persistent strong, tapering root produces lateral roots at an early stage. It has fifteen xylem poles in the stele. /

stele.

LATANIA COMMERSONII

GATIN figures only the initial stages of germination. The seedling described below produced its first aerial part, viz. the first and second leaves, nearly a year after sowing, but germination doubtless took place many months previously. Germination is hypogeal, non-ligulate (Fig. 130). The nut-like seed, flat on one side and convex on the other was 3 cm. long. The cylindrical stalk emerged as in other seedlings, by a spherical aperture bordered by two collars, one brown, the outer white. The stalk was 3 cm. in length. The cotyledon sheath was 5 cm. and the root 10 cm. long. The latter had given rise to numerous stout lateral roots and was woody. The first leaf has eight main and twelve subsidiary strands.

CHAMAEROPS EXCELSA

GATIN includes C. ^{humilis} ~~excelesa~~ in his list.

Germination. (Fig. 130).

Anatomy. There are four strands in the tip and the sheathing/

sheathing base of the cotyledon. They all enter the hypocotyl at the same level. The primary root is hexarch. There are nine main and ten subsidiary strands in the first leaf.

The suctorial tip of the cotyledon is soft, fleshy and spoon-shaped (Fig. 130).

COCOS CAPITATA

Of the three ovules produced in the fruit, one had aborted. The radicles of the two embryonic plants emerged by a clean cut circular aperture through the hard wall. At the early stage examined the lengthy portion of cotyledon from the plumule to the tip was solid. It elongates upwards to accommodate the laterally projecting plumular bud. GATIN found ligulate and non-ligulate germination in different species of *Cocos*.

For anatomy see Figs.

find references

ARECA SAPIDA

The seed is protected by a fibrous covering. Germination is hypogeal and ligulate. Six strands proceed from the tip of the cotyledon. Eight strands are found in the transverse section of the ligule, so at/

at least four of the strands must enter the ligule. Of the two strong and equally developed roots, it was impossible to determine which was the radicle. Both produced numerous short lateral roots, and the stele in each case was schlerotic. One root was pentarch, the other hexarch. GATIN describes Phoenix dactylifera and Trachycarpus excelsis^a, the other two seedlings which were examined. X

LITERATURE ON THE SEEDLINGS OF PALMS.

KLEBS places the Palms in Type I.; but since every type of germination is represented in the family, his treatment of them is inadequate. SCHLICKUM described the anatomy of the seedling of Washingtonia robusta: he found six strands in the cotyledon stalk and five in the sheath, while the ligule (for it belonged to the class of ligulate cotyledons) was supplied by two strands ascending to the tip and descending. A third strand died out at the apex of the ligule. DRABBLE examined Palm seedlings for the purpose of supplementing VAN TIEGHEM'S notes on the transition phenomenon. He disagreed with the latter and with SARGANT who classified the transition of Phoenix dactylifera as Type I. As for the/

the transition in general of Palms, he remarks that the plumular strands are later in differentiation and lignification than the cotyledon bundles, which is to be expected since the cotyledon functions earlier; at the same time, however, some of the xylem and phloem strands of the root are directly and primarily continuous with those of the plumule and have no connection or only a lateral one with strands common to root and cotyledon. The numbers which he gives are of interest. The root stele of *P. dactylifera* and of *Livistona* have twelve poles. While the cotyledon of the former may have six or seven strands that of *Livistona* has as many as fifty in the suctorial tip, but only nine in the sheath. *Oreodoxa*, *Pritchardea* and *Coleospadix* have essentially the same anatomy. In the suctorial tip of *Livistona* there is little xylem, a statement which recalls the more recent work of DIXON and BALL. They found that in the suctorial tip of the cotyledon of *Lodoicea sechellarum*, the proportion of phloem to xylem was in the ratio 8:1, the xylem being almost vestigial. It is a matter of interest that in this species of *Lodoicea* the seed weighs from twenty to twenty five pounds, and connection is maintained between seed and plant for five years. THISELTON-DYER (122) describes a similar/

similar case of a seedling on a large scale in his account of the germination of the Double Coconut, the cotyledon stalk being frequently four to five yards long, lying parallel to the surface.

SARGANT (103) believes the external and internal structure to have been profoundly modified by the arborescent habit since the primary root is well-developed and persistent, and in some (e.g. *Thrinax*) the first cauline root, the direct prolongation of plumular traces, surpasses it in length and thickness. She describes the transition from stem to root for species of *Thrinax*, *Desmoncus*, *Areca* and *Acanthophoenix* as well as the classic *Phoenix dactylifera*, finding large numbers for root poles and cotyledon strands and lays some stress on the two-fold symmetry of some and the bifid apex of the suctorial tip of *Chamaerops humilis* and *C. Fortunei*. GATIN questions the validity of the two latter features as evidence of the double-bundle theory.

GATIN'S research was concerned chiefly with descriptions of the embryo, germination and type of cotyledon. Although figures are occasionally given for root steles, and cotyledonary sheaths there is not the emphasis attached to transition phenomenon as one finds in SARGANT'S and DRABBLE'S publications. The introduction/

introduction to his work is a summary of the literature on Palm seedlings from 1588 to the year of his own publication (1906). No attempt will be made here to give an account of such investigations. The conclusions reached by GATIN are of such importance that a brief resumé will be given of them. No reference to them has been found in the literature consulted on seedling structure.

(a) There are three types of embryo in the Palmae:-

- i. where axes of plumule and radicle are straight (i.e. in the same straight line) and in the axis of the entire embryonic body;
- ii. where axes of plumule and radicle form a straight line not lying in alignment with the embryonic body, but oblique to it;
- iii. where the axis of plumule is at an angle to that of the radicle ("Embryons à plantule courbe").

The embryo is not surrounded by a continuous epidermis: it is interrupted by the cotyledon slit and the cavity left by the suspensor. Two or three leaves of the plumule are differentiated. A piliferous layer, developed late, may or may not be present, but a root cap is characteristic of all the species examined. Cortex and root cap are differentiated last in the embryo.

(b)/

(b) The morphology of germination is directly connected with the structure of the embryo,, as classified above.

- i. gives the "rémotive" type as in Phoenix, i.e. hypogeal non-ligulate;
- ii. produces a type where the cotyledon sheath provides laterally a little hood for the slowly developing plumule bud, e.g. Cocos capitata;
- iii. gives the "admotive" type, i.e. the ligulate cotyledon as in Areca sapida.

It is thus possible from an examination of the embryo to predict the type of subsequent germination. GATIN describes the increase in volume of original embryo cells and the cell divisions which must take place in restricted portions of the cotyledon in order that the seedling take its characteristic form. In the "admotive" type active cell division and not elongation of cells originally present is the potent factor in the production of the ligule. He remarks that whereas in type (i) above elongation of the cotyledon stalk takes place by growth in length of cells and sub-division, such is absent or less marked in the ligulate type.

GATIN'S general considerations take the form of a comparison between Palms and other monocotyledons. He compares the embryo and germination of the "admotive"/

"admotive" or ligulate type with those of the Grasses and Scitamineae while the "remotive" or non-ligulate type approaches the Aroids not only in the seedling form but in the embryonic structure, e.g. origin of the piliferous layer and nature of the radicle. The germination of Palms exhibits two phases: the first where the embryo elongates and emerges without cell division occurring ought to be considered not as the first stage of germination, but as the completion of the maturation of the embryo. The first phase does not occur in the Gramineae, for differentiation has proceeded so far, in the seed, that the parts of the embryo have already changed their relative positions, on the point of germination. The second phase of germination in the Palms, in which plumule and radicle, ligule of cotyledon if any, and axis take up their permanent positions in relation to one another, corresponds to the germination of the grasses.

GATIN believes the Palms to furnish evidence in favour of JUSSIEU'S theory that the cotyledon is the first leaf of the plant, but disagrees with SARGANT'S suppositions that symmetry of the cotyledon strands and shape of the suctorial tip have more than an intrinsic value.

DISCUSSION/

DISCUSSION ON SEEDLINGS OF SHRUBBY
AND ARBORESCENT PLANTS.

The following points emerge from the study of this group and a consideration of the literature -

- (a) The size of the seedling has a direct relation to the size of the seed. No exact comparison was made, however, of the size of the different embryos at maturity or between the size of the seedling and the bulk of endosperm available. Absorption of endosperm is rapid in the Liliaceae, rather slow in Vellozia and exceedingly slow in Palms. The attachment of cotyledon to the seed may last for months and even years in the latter group.
- (b) The primary root is lengthy, very strong and long lived. It early shows signs of becoming sclerosed. It produces strong lateral roots and is supplemented in the first month by one or more lateral roots. In many Palms this cauline root is indistinguishable from the primary root and is often in direct continuation with the plumule, at no point being attached to the primary root axis or cotyledon strands.

Anatomically the radicle exhibits great variation. /

variation. In the small Liliaceous types the stele is triarch to pentarch. In the Palms it is frequently pentarch or hexarch, but may have fifteen poles.

- (c) Development of the plumule is at the normal rate for the Liliaceae with the same type of germination, in those arborescents of the family described. In the case of Vellozia, it is slower. In Yucca and Dracaena it is unusually rapid according to SARGANT. The Palms show very strong development of the early leaves. While it has been suggested (103) that the habit of these plants may be connected with the rapid production of leaves, the fact that germination in the vast majority of cases is hypogeal cannot be overlooked as a contributing factor to the importance of the plumule. Even in the young seedling it has been found that plumular traces may be inserted directly on the root axis having no connection with cotyledon or hypocotylar strands. The possession of a cauline root devoted entirely to supplying the plumule is mentioned above.
- (d) Hypocotylar Structure affords an instance of an anatomical feature common to all but one seedling of/

of the group investigated in the present study, and to numerous examples in the literature. This is the vascular arrangement in which plumular and cotyledonary traces tend to run separately through the hypocotyl without anastomosing, even when the strands are surrounded by a sheath. This has been explained as a device to allow for increasing girth of the plant, and an increased number of plumular strands (103). In *Cordyline Banksii*, the exceptional case, the hypocotyl has root structure.

- (e) Type of germination is by no means constant; even in the one genus (e.g. *Cocos*) it is variable. Epigeal germination is the exception; *Cordyline* furnishes the only example in this investigation, and no other instance is recorded elsewhere. Of the hypogeal types all variations are possible. Ligulate and non-ligulate types occur almost equally. Of the non-ligulate type, the cotyledon as a rule is tubular merging into a short or fairly long stalk and distal suctorial tip, usually cylindrical save in the Palms in which the sucker may be spherical, concave or egg-shaped. The bifid shape in some is related to the need for/

for a greater surface, it would seem, rather than to phylogenetic considerations. In some non-ligulate types the cotyledon arches laterally to protect the elongating plumular bud; this occurred in the slowly developing Paris in the rhizomatous group.

As GATIN points out the ligulate germination is determined by the form of the embryo. The significant question as to the factors involved in the shaping and configuration of the embryo will be dealt with, as far as possible, in the final discussion.

- (f) The anatomy of the cotyledon is as variable as the morphology. The Liliaceae may have the double bundle type of vascular structure as in *Cordyline* and *Astelia*, or numerous strands as in *Yucca* and *Dracaena*; size of seed or size of the adult plant or both are probably making their influence felt. In the Palms as far as is known the strands in the cotyledon sheath are four to nine in number. The ramifications in the cotyledon tip and the preponderance of phloem over xylem often seen in such organs would suggest that the number of vascular strands is related to the/

the quantity of endosperm which has to be translocated. The need for more exact quantitative work on this point is apparent. That large numbers associated with the cotyledon is not peculiar to seedlings of arborescents is evident on recalling seedlings of Amaryllidaceae of the Crinum grouping.

- (g) While the seedlings of Palm show a very robust habit, this is lacking in the seedlings of Liliaceae examined, but is evidently appropriate to those of *Dracaena* and *Yucca*.
- (h) The seedling of *Vellozia* is in a category of its own. It resembles in no respect the arborescent *Doryanthes* of the same family, described by SARGANT (103). The delicacy of its appearance, retarded development, extremely simple vascular anatomy would make it appear, that, for the purposes of the present investigation, *Vellozia* would have been more suitably classified with seedlings of plants showing marked xerophily. Most of the features which go with the arborescent habit have been swamped by the expression of xerophytic characters in the seedling. The very slight/

slight indication of its affinities with other tree forms, given by the hypocotyl and, less obviously, the radicle, would be, by themselves, totally insufficient in an attempt to forecast the adult form from the structure of the seedling.

- (i) SARGANT'S statement that the arborescent habit has profoundly modified the external and internal structure will be discussed later.

D I S C U S S I O N.

The COTYLEDON as a BASIS for COMPARISON

The most important diagnostic feature of the phylum under consideration is the single seed leaf. Accordingly it may be profitable to discuss which feature of the cotyledon has most significance as a basis for making comparisons.

1. The cotyledon tip - is influenced by two sets of factors -

- (a) Factors influencing the shape involving the nature and quantity of the endosperm and the size and configuration of the seed.

- (b) Factors influencing the vascular anatomy.
Since the vascular supply is a response to physiological demands, the nature of the organism regulating such demands will affect the suctorial tip correspondingly.

Where the number of strands in the tip exceed three or four it is usual to find them ramifying without apparently obeying any law. In the Palmae and Cannaceae the number of strands seen in transverse section varies according to the region of the tip cut; the number diminishes towards the micropylar end. As a rule these traces are arranged/

arranged peripherally, their position being obviously related to their function. For these reasons it is inadvisable to attach any phylogenetic importance to the shape or internal structure, although two instances of attempts to do so are recorded (9, 103).

2. Base of the Cotyledon. The number of strands in the base tends to be constant for a species though not always for a genus. In the "bulbous" seedlings the number of strands increase as the bulb extends in girth. Hence the original strands ramify as additional vascular tissue becomes necessary.
- (c) The ligule - the vascular anatomy is slightly variable even in a genus. A further difficulty is the complicated appearance in cross section.
- (d) The stalk of the cotyledon is a convenient portion for comparison of the vascular anatomy in those instances where the number of strands is variable, throughout the length of the cotyledon. Although the length of the stalk is affected by the depth of sowing, as in the *Commelinas*, or the circumstances of germination as in the case of the viviparous *Iris Germanica*, the vascular anatomy does not alter.

THE MORPHOLOGY OF GERMINATIONThe Classification of the Germination of Monocotyledons.

Apparent differences in germination and the morphology of the seedling are directly due to the differences in the cotyledon. It has been suggested in the preceding pages () that the apparent diversity in the germinations is mainly superficial, and that classifications which emphasise the differences not only lead to confusion, but tend to obscure the true nature of the principal organ involved, namely the cotyledon.

The work of KLEBS was valuable as a record of the germination of a large number of seedlings, and is still quoted as a reference when a short description of germination is given. While it was the first classification in which any reference was made to the habitat and other factors that might influence the seedling, it suffered from the following defects -

- i. The length of the cotyledon stalk which has been demonstrated as being subject to conditions of germination, and therefore variable, was given a diagnostic value.
- ii. No distinctions were made between seedlings having/

having ligulate and non-ligulate cotyledons for both types appear in one group.

- iii. This cannot be regarded as resulting from an opinion on KLEB'S part that ligulate and non-ligulate cotyledons were exactly equivalent, for the relation of one type to another is not discussed.
- iv. Ligulate cotyledons are figured in seedlings of Type I as well as Type IV, while the Grass seedling is placed in a section of its own.

The tendency to disregard possible relationships is shown by more recent writers, CHOUARD differentiates between the form of cotyledon shown in hypogeal and epigeal germination, emphasising that these are separate types. These he sub-divides according to the proportion of sheath and stalk, taking credit for having first made the observation that such different types occur within one tribe, although GATIN, twenty years previously, discovered that in the Palms type of germination can vary within a genus.

From a survey of the seedlings described in the preceding pages it is evident that a rough distinction can be made between seedlings with a ligulate and those with a non-ligulate cotyledon. This division has a certain correspondence with the type of germination for/

for ligulate cotyledons invariably are associated with hypogeal germination, while non-ligulate cotyledons may be either.

THE NON-LIGULATE COTYLEDON

If the germination is epigeal, then the region between the base and tip of the cotyledon elongates carrying the seed upwards on its tip. If hypogeal, the same region elongates but in such a manner as to force the plumular bud deeper into the soil, a work in which it is assisted, as a rule, by contractile radicle.

Morphologically the two types are identical. Physiologically there is the distinction that in the epigeal type the cotyledon manufactures food in addition to conducting it. For this reason the photosynthetic region may appear elaborated, particularly in those instances in which, for a season, it acts as the only green leaf. This tendency is foreshadowed in the narrow lamina of *Nomocharis*; *Lilium* shows a comparatively broad "blade", while *Paris* is the best example of a persistent leaf-like cotyledon. Since plants possessing such leaves are specialised for geophilous conditions, it seems reasonable to suppose that this type of epigeal cotyledon is to some extent advanced.

Relation/

Relation between Type of Germination and Plumular Development.

In order to allow of the hypogeal cotyledon dispensing with photosynthesis, one or both of two possible methods to ensure adequate food is resorted to.

- i. There is a more rapid development of the plumule than in the epigeal type. To take as exact a comparison as possible a tribe exhibiting both types of germination may be cited. CHOUARD found that *Scilla bifolia* and *Endymion nutans*, both of the tribe *Scilleae*, are respectively epigeal and hypogeal. The production of foliage leaves takes place more quickly in the hypogeal seedling.
- ii. The amount of endosperm available (depending chiefly on the size of seed) may be large. In the Araceae the emergence of the first green leaf may not take place for some time.

It is not difficult to imagine that the two types of non-ligulate cotyledon, epigeal and hypogeal, have sprung from a common origin, or that one has been derived from the other. In the latter contingency the question as to which is the older type naturally arises. Taking the bulbous group as furnishing evidence/

evidence it will be remembered that plants with small light seeds had epigeal germination. The heavy seeds of the Amaryllidaceae were associated with hypogeal germination, although frequently there was some indication of the seed being pushed or pulled up through the soil. Apart from such considerations as the correspondence between advanced floral characters and type of germination, it seems evident that the problem of mechanics is a factor having considerable influence on the type of germination. A heavy seed which will entail difficulties in being raised into the air will, in all probability, contain either an embryo in a very advanced state of development, or an immature embryo lying in a copious supply of endosperm. The advantages of a plant having hypogeal germination would be -

- (a) added protection to the plumule;
- (b) more efficient anchorage. This has already been pointed out by SCHLICKUM.

The reason will now be apparent for terming the germination in the "bulbous" section as Type V. (as in KLEBS, with epigeal cotyledon) or Type V. hypogeal, the latter being merely a modification of KLEBS Type V.

THE LIGULATE COTYLEDON(a) Origin of the Ligule.

The origin of this type of cotyledon has been already touched on by SCHLICKUM (109), SARGANT and ARBEE (107). From the survey of a series of seedlings, beginning with a type such as *Commelina* with lengthy sheath and long stalk parallel to it, with an indication of a "hood" at the top, one may next consider the *Tigridia* type in which, possibly through further fusion of stalk and sheath where they tend to converge, the insertion of the "stalk" appears to be lower. Weight is added to the fusion argument from the behaviour of the vascular strand or strands, which, running to the top of the sheath, retrace their course parallel to, and for a great length in contact with their upward traces. In a ligulate cotyledon this actual fusion of upward and downward parts may not occur, as was seen in *Gloriosa*. The upward course then represents the strand of the original cotyledon sheath; the downward strand, its prolongation into and down a long stalk, which has now lost its identity save for an abbreviated portion, which may be inserted at any level on the sheath.

Seedlings of *Chlorophytum*
Tigridia/

Tigridia show the variability of the position of the stalk relative to the sheath. Apart from the Gramineæ, which are yet to be discussed, the Zingiberaceae show the culmination of the tendency to have the stalk inserted lower and lower on the sheath. That this tendency has a much deeper significance when the internal morphology is considered, will be apparent.

(b) Morphological Significance of the Ligule.

As already indicated, the hypogeal type of germination is, except in the "tuberous" group, correlated with rapid plumular development. The ligule may be regarded as a response to the need for a protective sheath which will elongate during the period when the first leaves need protection. But, it will be said, such a protection was just as adequately provided by the non-ligulate tubular type; the answer to which criticism will be found in -

(c) The Physiological Significance of the Ligule.

If a review is made ~~of the anatomy~~ of the cotyledonary anatomy of the ligulate types examined in this research, it will be seen that, while they occur once in Bromeliaceae (Billbergia), very sparingly in Amaryllidaceae (Alstroemeria), commonly/

commonly in Liliaceae, and very frequently in Iridaceae and Palmae, no other type is to be found in Cannaceae and Zingiberaceae. If, now, the vascular anatomy of the ligules be compared, it will be seen that when the cotyledon has numerous strands, as in *Canna* and some Palms, the majority of these enter the ligule. In the Liliaceae and Iridaceae both strands, or the single strand, enters the ligule, proceeds to the top and descends (e.g. *Merendera*, *Tigridia*, *Chlorophytum*). In the Zingiberaceae, however, as was pointed out in the discussion on that family either -

- i. both strands enter the ligule, but one ascends only a short distance,
- ii. one of the two strands enters the ligule, or
- iii. neither strand enters the ligule.

Here there is an obvious tendency towards reduction of the tissue in the ligule.

Before connection can be made between seed and primary root in the non-ligulate seedling, the vascular strands from the cotyledon tip must traverse the distance through a stalk and then down a sheath. This distance in a seedling where stalk and sheath elongate with the plumule, as in *Commelina* and *Iris germanica*, may be considerable; hence/

hence an extravagant expenditure of vascular material. The seedling of *Roscoea*, or better, *Hedychium* or *Alpinia*, shows an advance in having a more direct connection between endosperm, plumular traces, and root stele. There is no retrogression, for the plumular bud is as well, if not better protected than before.

(d) Use of the Term "Ligule".

The writer cannot give the first instance when this word was used for that part of the cotyledon sheath above the insertion of the stalk. In 1915, SARGANT and ARBUR preferred to use the term "upper sheath" for it. In the case of *Brachychilium*, where that part of the cotyledon outside the seed is all ligule, they simply called it "the sheath", presumably because there was no lower sheath. ARBUR uses it in 1925, in her chapter on seedlings, but makes no attempt to account for it. She remarks that the seed leaf may include "a ligule, which may be closed and tubular, and is then conveniently distinguished as a ligular sheath". From this it is evident that she would still consider an open short "sheath" not tubular as a ligule, (such, for example, as that slight prolongation upwards of the sheath seen in *Aloe*, and/

X and that recorded by GATIN for Anthurium and named by him "ligule" - page). While such instances do show the tendency for extension upwards of the cotyledonary sheath, they were not termed "ligulate" in the present work, for the following reasons -

- i. The term was reserved for seedlings truly hypogeal. The open sheaths referred to, occurred often in seedlings with the cotyledon partly above ground.
- ii. Such an upward prolongation is due merely to elongation of the cells, and not to cell division. In the true ligulate type as GATIN (48) has pointed out, the ligule arises and increases in length by cell division as well as by elongation of individual cells.

The use of the word "ligule" is somewhat unfortunate. While it is preferable to have a single word rather than "upper sheath", the term has already too many associations. The ligule of the foliage leaf, for example, is regarded by ARBER as the "upward winging of a tubular leaf sheath", by GLÜCK as fusion of adnate stipules. The so called "ligule" of the cotyledon, as has been demonstrated by/

by recourse to internal structure and a comparison of transitional forms, is neither. It is part of the sheath itself.

(e) Connection between ligulate germination and the embryo.

The present study was concerned with post-seminal developments. Accordingly, few sections were made of the embryonic condition. It was observed, however, that if plants having ligulate and non-ligulate cotyledons, e.g. *Brachychilium* and *Bowiea*, were longitudinally sectioned at a day old, before there was any sign of ligular development on the part of the former, a striking dissimilarity existed between them. Apart from differences in the degree of plumular development, the orientation of the vascular tissue and the configuration of the seedlings were different. In the non-ligulate type a straight line represented the connection between plumular bud and root cylinder. The seedling had a vertical axis. In the ligulate type the vascular tissue between plumule and radicle was in a gentle curve. As development proceeded, the plumule withdrew itself entirely from the horizontal position, became/

became vertical and was in alignment with the root stele, the ligule arching up as it did so.

It was, therefore, with great interest that a publication by GATIN, which has been referred to in the section on Arborescents, was read within the last few weeks. GATIN discovered that if the embryonic plumule and radicle lay at an angle to one another, i.e. if the vascular trace connecting them was curved, then the cotyledon was ligulate. Similarly, if the radicle and plumule lay in a straight line, the cotyledon was non-ligulate. The possible significance of this connection will be suggested later in this discussion.

(f) The Ligule of Costus and other Cotyledonary Outgrowths.

- i. Costus. From the interpretation just given of the ligule, it follows that the ligular outgrowth on Costus, which is non-vascular, is either the vestige of a much longer ligule where the term has the significance of part of the cotyledonary sheath. The stalk would then have to be visualised as having become flattened to take on photosynthesis. The cotyledon then adopts a compromise by which the plumule has protection as in the hypogeal type, while the cotyledon/

cotyledon carries on the work of a leaf as in the epigeal type. The second suggestion which, from the nature of the origin of the ligule seems nearer the truth of the matter, is that an instance is provided in which the cotyledon has taken on a feature of the adult leaf of the plant, namely a ligule (the term here having ARBER'S or GLÜCK'S meaning, previously referred to).

- ii. Aponogeton. The sheath wings at the base of the cotyledon (figured by ARBER, 3p. 158) seem to be of the same nature as the ligule of foliage leaves.
- iii. The upward arching laterally of the cotyledon sheath by a slowly developing plumule, as occurs in *Paris*, *Lilium*, *Bowiea* and some Palms, is not regarded as forming a ligular outgrowth, but merely a displacement of the sheath, for no vascular tissue is involved in the change. It must be recorded, however, that GATIN discovered that, to a small extent, cell division took place in the prolongation of the sheath, and that, in the embryo, the plumular axis was not in alignment with that of the embryonic body.

The/

The foregoing discussion points to the conclusion that there is no morphological difference between hypogeal and epigeal germination and, while cotyledons may be termed ligulate and non-ligulate for purposes of description, no essential distinction exists between the two types. Further, proceeding from the simple to the advanced, the following series may be followed -

epigeal → hypogeal → ligulate cotyledon

THE/

THE EFFECT OF THE HABIT OF THE ADULT
PLANT ON THE SEEDLING STRUCTURE.

Its Effect on the Morphology of the Cotyledon.

If the groupings in which the seedlings were described be kept in mind, the following facts come to light -

- i. The hydrophytes, representing plants of seven families, have, without exception, epigeal cotyledons.
- ii. The bulbous type have non-ligulate cotyledons, which may be either epigeal or hypogeal. In the section having small seeds the tendency is for germination to be epigeal.
- iii. In the "xerophytic" group the succulent seedlings are all epigeal; the epiphytes show all types of germination and cotyledon.
- iv. With one exception, Cordyline, the Arborescents have hypogeal germination, the cotyledon being ligulate or non-ligulate.
- v. Only three genera of climbing plants were examined: Germination in each was hypogeal and ligulate in addition, in Gloriosa.

- vi. The seedlings of twenty seven species of cormic and tuberous plants were described. Without exception germination was hypogeal. Of the total number only six, five Iridaceous and one Liliaceous, had ligulate cotyledons. These, it will be observed, belong to the families having corms.
- vii. In the rhizomatous group the majority of ligulate cotyledons occur.
- (a) Of eleven Liliaceae only one, *Chlorophytum*, is ligulate.
 - (b) All species of *Canna* referred to are ligulate.
 - (c) All species of Zingiberoideae referred to are ligulate.
 - (d) The only genus of Amaryllidaceae mentioned is ligulate.
 - (e) The Commelinaceae are non-ligulate, but with a tendency to form ligules.
 - (f) Four genera were represented by the Iridaceae. Germination of both types occur. *Iris ensata* provided the only instance of a ligulate cotyledon, but in the hypogeal members of this group the tendency is for arching of the sheath to occur so as to suggest the formation of a ligule.

From a review of the above results the following suggestions may be made.

1. The aquatic habit seems to favour epigeal germination, possibly because the danger of dessication/

dessication of the young organs is at a minimum, and there is no necessity for short cuts in the water carrying system.

2. Plants with perennating organs such as bulbs, or tubers which arise with their axis in alignment with that of plumule and radicle of the seedling, have hypogeal or epigeal germination, but invariably non-ligulate. Trillium and Paris, with rhizomes which are of the nature of vertically placed tubers for one season follow this rule. It may be that the asymmetry or restrictions on girth imposed by a low insertion of the cotyledon stalk does not encourage the bulbous habit. The axis of plumule, cotyledon and radicle of seedlings having the bulbous habit tends to be a vertical straight line, save in the instances where a heavy seed keeps the stalk of the cotyledon bent.

3. Hypogeal germination of the Arborescents and Climbers may be reasonably attributed to the necessity for exceptionally good anchorage.

4. The tendency for hypogeal germination in the group of corms and tubers is, doubtless, correlated with the same need. If the question arises why all bulbous plants do not behave similarly, the constant presence of a strong contractile primary root in the bulbous group supplies an explanation.
5. It has already been mentioned that there seems to be no relation between the epiphytic habit and hypogeal and epigeal germination. But the specialised nature of the family of the Bromeliaceae is reflected in the peculiarities in the germination and seedling.
6. The rhizomatous group shows variabilities in having examples of both types of germination and cotyledon. One reason may be that this grouping was heterogeneous, since the habit occurs in all families. It was to be expected that, in a survey of such markedly different families as Liliaceae and Zingiberaceae, some indication of family characteristics would be apparent. Such characteristics will be discussed under a separate heading.

THE EFFECT OF HABIT ON DEVELOPMENT
OF THE PLUMULE

(a) Tuberous and Bulbous Types.

Retardation in plumular development in the Aroids is related to absorption and conduction to the tuber of reserve food which would otherwise be available for the plumule. *Arum maculatum* presents an instance of exaggerated delay in the appearance of the foliage leaves. In the *Medeolae*, *Lilium* and *Bowiea* bulb formation seems to be of primary importance. The chances of success are apparently ensured by the provision first of a bulb, and not by the early production of leaves.

(b) Xerophytes.

The poor development of plumule in seedlings such as *Aloe*, *Dyckia*, *Puya* is to be related with the tendency of the adult plant to reduce the leaf area as far as possible.

The abnormally weak plumule of *Bowiea*, which may be explained by bulb formation, may also be related to that aspect of the xerophilous habit by which the leaves are reduced to mere scales: this occurs in the leaves of the climbing axis of the adult plant.

(c)/

- (c) The hydrophytes produce their first leaves at a rate which is neither fast nor markedly slow.
- (d) SARGANT records that arborescents have unusually strong and rapid development of the plumule. This was not observed in the genera examined. In the group of climbers, however, the dominant organ is the plumule which develops rapidly.
- (e) Plumular development is more advanced in hypogeal than in epigeal types. When the cotyledon is ligulate the plumule is dominant even in a day-old seedling. The first leaf emerges within a few days and uniform progress is made at a rapid pace thereafter. This correlation between the ligulate cotyledon and remarkable plumular development will be again referred to.
- (f) The general form of the seedling indicates in some measure the habit of the adult. The xerophytes have the rosette habit, the aquatics a close-tufted habit, once the early leaves appear.

THE EFFECT OF HABIT OF THE ADULT ON THE
DEVELOPMENT OF THE RADICLE.

- (a) The aquatics are characterised by a radicle which
at/

at first does not elongate, but is assisted by a collar of strong root hairs arising a short distance behind the root tip. As the plumule develops the primary root elongates.

- (b) A persistent primary root assuming a contractile function is found in bulbous and tuberous plants. It may be the only root for the first year, or it may be assisted by only one cauline root. In xerophytes it tends to be very long and tapering.
- (c) The radicle of many arborescents is long lived. In such ^{the} stele becomes sclerosed in many instances. Numerous lateral roots are produced from the tap root.
- (d) In the group of climbers in particular the radicle is remarkable for its length and the development of the central cylinder. The rope-like arrangement of the root system of *Gloriosa* seems to be unique.
- (e) Seedlings having epigeal germination, i.e. hydrophytes, bulbous, tuberous, and a few rhizomatous plants, have for the first few weeks, and frequently for a longer period, a tap root. In the ligulate types, beginning with transitional forms such as/

as *Commelina* and proceeding to the advanced ligulate forms, as in *Zingiberaceae*, the primary root is decreasingly developed until in some genera it is not produced as a separate organ, although its vascular tissue is present in the embryo. Such is the case in *Canna* and some *Zingiberaceae*. The lack of the primary root is made good by adventitious roots, the meristem for which is laid down in the embryo.

Since the great majority of seedlings having ligulate cotyledons are rhizomatous, the poor development and short duration of the primary root may be correlated with the rhizomatous habit, one feature of which is an adventitious root system in the adult plant. The adventitious root system arises in response to the demands of the plumule, which may, therefore, indirectly affect the radicle. The most marked example of the primary root being affected by the adult habit is seen in the epiphytes in many of which a radicle is entirely lacking.

The conservatism of the root makes it the more striking that it should be affected by the habit of the adult.

THE HABIT OF THE ADULT AND
ITS EFFECT ON THE HYPOCOTYL.

If the type of germination be related to the habit, then the hypocotyl must also, to some extent, be connected with it.

The hypocotyl has its highest development in the tuberous and cormic group in most of which it becomes swollen for food storage. The effect of this on the vascular structure has been seen. True tuberosity is purely secondary. It never appears in the embryo.

Where the hypocotyl supports leaves early, it has stem structure. In two seedlings, *Arthropodium* and *Cordyline*, it had root structure in the stele, but no other characteristics of the typical root.

The hypocotyl, as a distinct region, was lacking in the bulbous group, and in all instances of definitely ligulate cotyledons save *Chlorophytum*.

The study of the *Commelinaceae*, *Iris germanica* and *Chlorophytum* confirms EVANS' observations that the length of the hypocotyl depends on the depth of sowing. If the plumular bud is too deep in the soil, the hypocotyl elongates. The length of the hypocotyl is, therefore, related to the environmental conditions of the seedling, not of the adult plant. It does not appear as a definite region where the plumule has to be pulled deeper in the soil (e.g. bulbous), but only where the plumule must be forced towards the surface.

THE EFFECT OF THE ADULT HABIT ON
INTERNAL STRUCTURE.

The Cotyledon.

Phylogeny must loom so largely in any consideration of internal structure that it is impossible to identify anatomy solely with the habit for a particular plant.

- (a) Hydrophytes. The constancy of the single vascular strand, enclosed in a strong sheath and proceeding through an aerenchymatous cotyledonary lamina occurs not only in the seedlings described in this thesis, but in *Luzula*, *Juncus*, and the *Cyperaceae*.

BEWS has remarked (*q*) that, in moist situations in the world to-day, which are not dominated by woody Dicotyledons, grasses and sedges hold sway, and that such marsh types are widespread owing to the "Uniformity and ancient unchanging character of the habitat". Three suggestions then as to the uniformity of the seedling, and the cotyledon in particular, may be put forward -

- i. The vascular anatomy has reached a state of almost extreme reduction as a consequence of/

of the habitat.

- ii. The families represented are primitive families, and the vascular anatomy at no period was more developed than it is at present.
- iii. The simplicity of anatomy is not the result of the habitat, but the plants being unadaptable have been forced to colonise a habitat which will not demand of them too great a specialisation of the vascular tissues, and having been successful in it for the reason put forward by BEWS.

- (b) Epiphytes. It is unreservedly admitted that the Bromeliaceae are a family representing a "specialised class of derivative forms which have responded to the effects of the organic environment". The argument for reduction, as a result of mode of life, can be more legitimately used of their seedlings.
- (c) The extreme xerophily of Vellozia seems also to be reflected in its structure, but the alternative suggestion of primitiveness cannot be neglected.

(d) /

(d) Cotyledons with many strands are characteristic of the Palmae, Cannaceae, Amaryllidaceae having bulbiform seeds, certain arborescent Liliaceae, the Araceae and Hemerocallis (p. 2). It is difficult to decide to what extent the adult form is responsible for such cotyledons.

- i. Differences in cotyledonary structure in seedlings of plants of similar habit are definitely referable to differences in size of seed.
- ii. Large seeds are produced by arborescents, the seedlings of which are therefore influenced by the habit of the adult.

If, as COMPTON argues, the arborescent habit is primitive (29) then this type of cotyledon is primitive. More simply, the cotyledon may repeat in its anatomy the vitality of the fully grown plant. This view includes the cotyledonary structure of Araceae.

(e) The bulk of the "rhizomatous" and "bulbous" groups have two strands in the cotyledon. Little can be argued from a number lying between the extremes associated with arborescents and epiphytes, although SARGANT and ARBUR regard it as the/

the indication of a central type.

Relating the anatomy with the possible habit of such types, one can only deduce that conditions of living and the size of the adult plant are of such a nature that they are neither subject to the rigours of a life leading to extreme reduction, nor to the necessity for retaining as much vascular tissue as possible to meet the strain of building up an adult with the size and structure of an arborescent.

The Root.

In general there is a direct relationship between the number of cotyledonary strands and the number of poles in the root stele. Root structure is affected by the habit of the adult in the same measure then, as the cotyledon. Where the root structure is of paramount importance, e.g. in climbers, a direct correlation with the habit exists. The same applies to examples of extreme reduction.

The Hypocotyl.

Its structure is noticeably influenced where tuberosity will occur, and in arborescents, in which the plumular and cotyledon strands are independent in the hypocotyl, an advantageous arrangement which allows extension of the vascular system and increase in girth, with the development of aerial parts.

TABLE I.
GENERAL SUMMARY

	Germination	Cotyledon	Strands in Cotyledon	Poles in Root Stele	Leaf	Habit of Adult
<u>HELOBIACEAE</u>						
Aponogetonaceae	E	-	1	1 or 2	3	} Hydrophytes
Juncaginaceae	E	-	1	1 or 2	3	
Alismaceae	E	-	1	1 or 2	3	
<u>SPADICIFLORAE</u>						
Palmaceae	E and H	L and N	4-15	6-15	-20	Arborescent Tuberous
Aroideae	H	N	5-9	2-6	3-8	
<u>FARINOSAE</u>						
Eriocaulaceae	E	N	1	2	3	Hydrophytes Rhizomatous Epiphytes Hydrophytes
Commelinaceae	H	N	2	3 or 4	5-7	
Bromeliaceae	E and H	L and N	1	1	3	
Philydraceae	E	N	1	1	3	
<u>LILIIFLORAE</u>						
Liliaceae	E and H	L and N	2-3	2-5	3-	Various Bulbous
Amaryllidaceae	(E and H)	N	2-4	3-4	3	
Dioscoreaceae	(H	N	5-10	5-10	5-9	

<u>LILLIFLORAE</u> (contd.)						
Dioscoreaceae	H	N	double bundle	4	5	Tuberous
Iridaceae	E and H	L and N	single or double bundle	2- 4	2- 7	Various
<u>SCITAMINEAE</u>						
Zingiberaceae (excluding Costus)	H	L	2	3- 4	3	Rhizomatous
Cannaceae	H	L	7- 9	-	11-20	Rhizomatous

NOTE:

E = Epigeal germination
H = Hypogeal germination

L = Ligulate Cotyledon
N = Non-Ligulate Cotyledon

TABLE II.
L I L I A C E A E

Germination	Ligulate	Non-Ligulate	Cotyledon	Root	1st Leaf	Habit
-	-	X	3- 5	4- 7	-	Climber
-	-	X	3	7- 8	3- 5	Climber
-	-	X	5	5- 6	10 3- 5	Rhizomatous
-	-	X	2	4		
-	-	X		5		
-	X	X		5		
-	-	X		5		
-	X	-	2	2,4,6	3- 5	Succulent
-	X	-	2	2	3	
E	-	-	2	3	3	Arborescent
-	X	-	2	4	3	
-	-	-	3-10	6- 7	6-11	
-	-	-	3 D.B.+ 1	18		
Anemarrhena/						

Asparagus

Lapageria

Hemerocallis

Blandfordia

Phormium

Kniphofia

Hosta

Aloe

Gasteria

Cordyline

Astelia

*Yucca

*Dracaena

Anemarrhena/

Germination	Ligulate	Non-Ligulate	Cotyledon	Root	1st Leaf	Habit
Anemarrhena	-	X	2	-	-	Bulbous
Asphodeline	-	X		-	-	"
Fremur	-	X		-	-	"
Bulbine	-	X		-	-	"
Chlorogalum	-	X		-	-	"
Anthericum	-	X		-	-	"
Bowiea	-	-		-	-	"
Pasithea	-	-		-	-	"
Arthropodium	-	-		-	-	"
Chlorophytum	X	-		2, 3	5	Rhizomatous
Brodiaea	-	X	2	2	-	Corm
Erythronium	-	X	3	3	-	Bulb
Ornithogalum	-	X	3, 4	3, 4	-	
Scilla	-	-	2	2	-	
Lachenalia	-	X	3	3	-	
Fritillaria	-	X	2	-	-	Bulb
Lilium	-	X		4	3	
Merendera	X	-	2	3- 4	5	Corm
Gloriosa	X	-	2- 4	2- 4	9	Climber
Paris	-	X	D.B. plus 2 laterals	3	approx. 5	Rhizomatous
Trillium	-	X		3		

Note: A double bundle (D.B.) in the cotyledon is considered equivalent to two strands.
Sargent's results are marked *

THE RELATION OF THE SEEDLING
STRUCTURE TO TAXONOMY.

"The exact nature of the connection is yet undetermined.. Conclusions from the new embryology ... appear to conflict with the results of systematic botany ... It does not necessarily follow that embryological evidence is of no systematic value."

ETHEL SARGANT, 1914.

A study of the foregoing data, in table form, according to family, reveals certain relationships. The comparisons are made purely on seedling structure.

COHORTS.

1. There is no striking similarity between any two cohorts.
2. In general there is only a very slight correspondence within the cohort in the external morphology; anatomically the relationships are somewhat stronger save in the Scitamineae.
3. The cohort showing greatest uniformity is the Helobieae.

FAMILIES./

FAMILIES.

1. Certain families would have been more happily placed in another cohort; e.g. -
 - i. Eriocaulaceae, Philydraceae, with the Helobieae.
 - ii. Commelinaceae with its beautiful symmetry in form and vascular anatomy with the Liliaceae, although the precocity of its cauline roots and its tendency to the ligulate type recalls the Zingiberaceae.
 - iii. The relative size of embryo and endosperm and the many-stranded nature of the cotyledon would make fitting the grouping of Palms and Aroids. But the diversity in germination shown by the Palms is another justification for ENGLER'S separation of them into a cohort, the Principes.
 - iv. The similarity anatomically between the Helobieae and the Bromeliaceae would not, however, justify their being grouped together since, in addition to fundamental differences in the adult, others connected with the environment occur.
2. Within a family, the resemblance between the genera may be very close, such is the case in the hydrophytic families, in Cannaceae, Zingiberaceae, Commelinaceae, Aroideae and Dioscoreaceae. The diversity in form of the seedling of Liliaceae and Iridaceae reflects the heterogeneous nature of these families in all but the floral characters.

SPECIES.

Specific differences, as a rule, do not markedly affect the seedlings. In primitive families, however, (p.)/

(p. X) they may be considerable, involving the morphology of the cotyledon. Where there are strong generic resemblances in a family it is most difficult to differentiate between the species.

Variability is to be found in features such as the root stele, venation of the first leaf (Crocoideae), the nature of glandular hairs (Bromeliaceae), epidermal cells (Commelinaceae), etc.

The organ least affected by differences in species is the cotyledon. Its anatomy is invariable within a genus save where there are numerous strands, in which instance the anatomy may be variable even within the species. Fluctuation in the number of poles of the root stele then occurs, but to a less extent than in the cotyledon.

SEEDLING STRUCTURE as an aid to TAXONOMY.

DE FRAINE found the seedling structure was useless in delimiting the genera of Cactaceae, while LEE discovered that in Compositae vascular structure was variable even for a species. But the findings for families which, like Compositae, are in a state of flux, or for highly specialised xerophytes such as Cactaceae, cannot be extended to a phylum.

The following conclusions regarding the Monocotyledons may be drawn.

1. In families exhibiting uniformity, seedling structure/

structure does not define the genus.

2. Such families have seedlings so distinctive in appearance that the family is identifiable. Instances of this were furnished in the present research (p.).
3. Certain tribes are recognisable by their characteristic seedlings in families where the latter are subject to variation.
4. A scheme for the identification of a plant by its seedling would not be parallel to that founded on floral characters, but there would be a rough correspondence between the two if the taxonomic scheme had a phylogenetic basis. The same families would be advanced in both floral and seedling characters. Certain anomalies would mitigate against complete harmony between the two schemes.

Done
(a) According to systematists, the Glumiflorae present a primitive type. The closing stage in a long reduction series is shown in the seedling.

(b) The Orchidaceae are the culmination of evolution in the flower. The seedling is unique in its lack of differentiation (which may, however, indicate degeneration and not primitiveness).

(c)/

- (c) An advanced type of germination may occur in an isolated genus or species of a family which is primitive in floristic and seedling characters, and vice versa.
- (d) Unrelated forms may have the same seedling structure. In brief, evolution in the seedling, as a rule, keeps pace with advance in floral structure. The converse is less frequently true.

THE ONTOGENY OF THE SEEDLING.

The seedling anatomy may be of value in showing the primary condition of the stele, but it is apparent that the early stages in the ontogeny of the seedling are passed over too quickly to be helpful in making deductions.

A NEW INTERPRETATION OF THE MORPHOLOGY OF THE GRASS
EMBRYO, BASED ON EVIDENCE REVEALED BY THE PRESENT
INVESTIGATION.

"The embryos of Grasses have been examined more extensively, perhaps, than the embryos of any other monocotyledonous group."

COULTER, 1915.

I. HISTORICAL ACCOUNT OF PREVIOUS VIEWS.

The structure of the grass embryo is still the most controversial question in seedling morphology. The lengthy bibliography given by WORSDELL in 1916 testifies to the efforts made to elucidate the problem; but even WORSDELL'S list is incomplete, for, apart from short papers published within recent years, reference is not made to what was possibly regarded as the final verdict on the structure of the mesocotyl, namely SARGANT and ARBUR'S Memoir of 1915.

The grass embryo has been so often described that another account of it would be superfluous. The opinions of different investigators on the structures in dispute will be summarised.

The Scutellum. This fleshy shield-like structure, is now commonly admitted to be a haustorial organ, the equivalent/

equivalent of the suctorial part of the cotyledon.

It has been interpreted at different times as follows:-

- i. The single cotyledon - SCHLEIDEN (1846); VAN TIEGHEM (1872).
- ii. Axial in its nature - HOFMEISTER (1849, 1861); REGEL (1843); GRIS (1864).
- iii. The Tegument of the Endosperm - AGARDH (1858).
- iv. A haustorial organ but not morphologically comparable to the cotyledon - SACHS (1868).
- v. An absorptive organ - RICHARD (1811).
- vi. Part of the single cotyledon, the other part being the coleoptile. - CASSINI (1820); RASPAIL (1824); HANSTEIN (1870); HEGELMAIER (1874); FLEISCHER (1874); KLEBS (1881); SCHLICKUM (1896); VAN TIEGHEM (1897); CELAKOVSKY (1897); RENDLE (1904).

Coleoptile. This term designates the sheath of the plumule. It has been regarded as -

- i. the expanded part of the cotyledon - MIRBEL;
- ii. the single cotyledon enveloping the plumule - RICHARD;
- iii. a primordial leaf succeeding the cotyledon - SCHLEIDEN;
- iv. the single cotyledon - SACHS;
- v. exactly comparable to the ligule of the cotyledon of other monocotyledons - SCHLICKUM;
- vi. the union of a pair of stipules belonging to the cotyledon proper (i.e. scutellum) - VAN TIEGHEM.

Epiblast/

Epiblast - a parenchymatous non-vascular, leaf-like structure which may or may not be present. It is situated opposite to the Scutellum. It may be -

- i. A rudimentary second cotyledon, MIRBEL, BRUNS, COULTER;
- ii. A prolongation of the scutellum - RICHARD;
- iii. Part of cotyledon sheath - SCHLEIDEN;
- iv. A cellular outgrowth from the sheath or a second cotyledon - VAN TIEGHEM.
- v. A pair of fused auricles, the cotyledon being compared to the adult foliage leaf; the scutellum is regarded as the lamina, the coleoptile the ligule. CELAKOVSKY;
- vi. Part of the Coleorhiza, since it possesses a downward extension - SCHLICKUM.

Mesocotyl. The most weighty argument against the ligulate nature of the cotyledon is that in certain genera a region, produced by intercalary growth separates what is regarded as the two parts of the cotyledon, viz. scutellum and ligule, hence the name which was used first by CELAKOVSKY.

The discussion of the significance of mesocotyl is of more recent origin. The following views concerning it have been held.

- i. VAN TIEGHEM described it by a "bold morphological fiction" (107) as a lengthened node.
- ii. CELAKOVSKY from developmental evidence also believed it to be a much extended cotyledonary node./

node.

- iii. BRUNS, basing his argument entirely on external appearances regarded it as the first internode of the plumular axis, an opinion revived in recent years by COULTER.

II. PUBLICATIONS SINCE 1915 ON THE MORPHOLOGY OF THE GRASS EMBRYO.

- (a). COULTER, whose views were coloured by research on a dicotyledonous *Agapanthus*, attempted in 1915, to extend his observations on germination of Monocotyledons to the Gramineae. Like every other investigator he wished to bring the grass embryo into line with the typical Monocotyledonous example. Having previously expressed the opinion that "cotyledony in general could be reduced to a common basis in origin, the number of cotyledons being a secondary feature", he now demonstrated that grasses, as a whole, showed "a remarkable number of transition stages from dicotyledony to monocotyledony". The second cotyledon was naturally the epiblast; the mesocotyl between them was, therefore, the first internode of the plumule.

This publication was adversely criticised
by/

by WORSDELL in 1916 on two grounds.

- i. His conclusions, like BRUNS', were based on external appearances.
- ii. He ignored the previous publications of HANSTEIN, VAN TIEGHEM, SCHLICKUM and CELAKOVSKY. Thus the anatomy of the mesocotyl was entirely neglected.

Apart from this it may be criticised on the grounds that the writer, in searching for dicotyledony in such an embryo, showed an inadequate comprehension of its position in the evolutionary sequence.

- (b) WORSDELL reviewed the previous literature on the grass embryo. He remarks that there is absolutely no foundation for BRUNS'S and COULTER'S view that the mesocotyl is the first internode of the epicotyl, and that the coleoptile is the first plumular leaf. According to WORSDELL, the latter is part of the cotyledon and corresponds to the ligule of a foliage leaf: the mesocotyl is the elongated primary node, while the epiblast corresponds to the auricles of the base at the lamina of the foliage leaf. The scutellum represents the lamina of the cotyledon comparable to that of the/

the grass leaf. His conclusions are arrived at by means of comparative morphological treatment in which the seed leaf is on a parallel with the foliage leaf.

WORSDELL'S theory does not account in a satisfactory manner for the internal structure of the mesocotyl.

- (c) SARGANT and ARBUR (1915) introduced a new method, using the cotyledon anatomy of other monocotyledons to lead them to a theory accounting for the anatomy of the mesocotyl. This region is traversed by a trace from the scutellum in addition to the plumular strands as BRUNS, LEWIN and SCHLICKUM had discovered.

By considering a series of seedlings such as *Commelina*, *Tigridia* and *Elettaria*, SARGANT and ARBUR conceived the idea of the stalk of the cotyledon becoming more and more closely adpressed to the sheath. Such a fusion could proceed further, affecting both cotyledon stalk and hypocotyl. The resulting structure would be characterised by both cotyledon and plumular traces, the former being inverted. This theory accounts for -

i. the origin of the mesocotyl;

ii./

- ii. its internal anatomy, which, with no further evidence than was available at the time, was otherwise inexplicable.
- iii. It confirmed the generally accepted opinion that the coleoptile, which surmounted the mesocotyl, was the homologue of a cotyledonary ligule comparable to that of *Elettaria*, or *Merendera*.
- iv. It accounted for the anatomy of the coleoptile, for the dichotomy of the cotyledon trace at the top of the mesocotyl resulted in two "ligular" strands passing into the coleoptile, supposedly similar to the two ligular strands in the *Zingiberaceae*.
- v. It was another effort to link up the morphology of the grass embryo and seedling with that of others of the phylum in the light of new information on the anatomy of the ligulate cotyledon.

On the other hand the objections which may be raised are -

- i. It failed to account for the epiblast.
- ii. It was based on a preconception that the coleoptile/

coleoptile was exactly homologous with the ligulate cotyledon. The writers were so biassed by the anatomical resemblance between the two that the facts concerning the mesocotyl were made to fit a theory which would allow the coleoptile to be such a ligule.

iii. It lacked simplicity.

The ligulate cotyledon was an advance on the non-ligulate type in that direct connection between cotyledon sucker and the hypocotyl was possible. According to SARGANT and ARBER'S Theory, the cotyledon of the grass seedling was retrogressive in that the course of the single strand was considerably lengthened (a) by having to proceed through the mesocotyl,

(b) by continuing to the tip of the ligule.

iv. It rested on insufficient evidence. A very thorough research was made on numerous grass seedlings, but the theory was founded chiefly on the vascular skeleton of six genera of Zingiberaceae. In four of these the two cotyledon strands entered the ligule, but in *Alpinia* the upper bundle when it entered the sheath only penetrated it for a short distance and/

and in *Brachychilium* the ligule contained no bundles whatever. The complete anatomy of all was not investigated. It was assumed that because the six seedlings were evidently built on the same plan, only a type need be described. The exact course of the strands which did not enter the ligule in *Alpinia* and *Brachychilium* was not followed. The fact that ligules were often non-vascular might have been a possible objection to their use as evidence for the nature of the two-stranded coleoptile.

- v. Explanations of certain structures had to be made, with some difficulty, for the sake of conformity with the theory. To the "xylem arch" connecting the scutellum trace with that of the plumular axis was allotted the purpose of water supply direct to the scutellum from the nodal roots.
- vi. The theory was based on the assumption of a fusion between cotyledon and plumular axis. "The (scutellum) trace represents the stalk and is the last vestige of its independence". Admittedly the stalk of the cotyledon may fuse/

fuse with its own sheath, and in certain genera the insertion of the stalk is so low that it may be regarded as fusing with the hypocotyl. But no instances were furnished where it could be claimed that the cotyledon stalk had fused with the plumular axis.

- (d) From a study of the ontogenetic development and structure of the embryo PERCIVAL (/) believes that scutellum, epiblast, coleoptile and first green leaf are the first four leaves of the plant. "The alternate distichous disposition of these structures on opposite orthostiches" and the arrangement of adventitious roots supports this conclusion.

This author fails to appreciate what SARGANT so clearly demonstrated, that the Key to the interpretation of the grass embryo was to be found not in itself, but in the structure of seedlings, the nature of whose organs was in no way obscure. The anatomy of the mesocotyl is again not accounted for. Further, as HOWARTH later pointed out "there seems to be no justification on anatomical grounds for thus far separating scutellum and coleoptile".

- (e) The most recent publication that has come to the writer's/

writer's notice is that on the seedling development of *Festuca rubra* by HOWARTH () in 1927, who found in this genus a type simpler than *Avena*, which SARGANT and ARBUR regarded as the simplest. HOWARTH, who agrees with WORSDELL on the nature of the mesocotyl, concludes that the name is singularly appropriate, and agrees with SARGANT and ARBUR that coleoptile and scutellum are parts of a single cotyledon, but thinks that direct connection of the scutellum trace with the mesocotyl stele ("xylem arch") is normal and not for the purpose that SARGANT and ARBUR suggest.

III. EVOLUTIONARY TENDENCIES IN THE MONOCOTYLEDONOUS SEEDLING.

If a survey be made of seedlings of the whole phylum but excluding Gramineae, certain trends are apparent.

I. From Epigeal to Hypogeal germination as evidenced

- i. by the relative numbers of each,
- ii. by a consideration of the families still retaining epigeal germination.

The weight of the seed as a possible factor in this evolutionary trend cannot be neglected.

II. From the non-ligulate to the ligulate type of cotyledon.

- i. /

- i. The greater number of species with the ligulate cotyledon tend to occur in the most advanced families.
- ii. Certain families, as a whole, are at the transitional stage, e.g. Commelinaceae.
- iii. The advantages of the ligulate over the non-ligulate type have been suggested, but on such grounds alone it cannot be claimed that evolution has proceeded in the direction of the more advantageous.

The fact that within one genus both types of germination and cotyledon can occur is no argument against these trends.

III. Towards increasing development of the plumule.

The fact that a cotyledon is hypogeal makes the early appearance of photosynthetic organs an urgent necessity unless endosperm is plentiful. Thus the plumular bud is increasingly developed at early stages. Even in the embryo its relative importance can be deduced from its state of differentiation.

IV. Towards decrease in importance of the radicle.

Just as the importance of the plumule is dependent on the germination, so is the development of the radicle connected with that of the plumule. In seedlings with ligulate cotyledons and exhibiting advanced differentiation and rapid growth of the/

the plumule, the primary root tends to be increasingly dominated by the latter until, in extreme cases, it does not appear as a distinct organ.

This tendency was seen by GATIN to affect the embryo. He was able to construct a series ranging between Alismaceae and Gramineae (page) in which, proceeding from the former, the pili-ferous layer became more and more endogenous.

Early adventitious roots compensate for the inefficiency of the primary root. Two suggestions regarding the limitations of the latter organ may be made.

- (a) The quantity of raw material and the space in the seed at the disposal of the embryo is, to a certain extent, fixed. If one organ, e.g. the plumule, develops very markedly, it must do so at the expense of another organ.
- (b) The rapid production of foliage leaves throws a considerable strain on the vascular system of a single primary root incapable of secondary thickening. Consequently it is advantageous for the leaves to have a water supply independent of the radicle. The intimate connection between the adventitious roots and the/

the plumule is clearly seen in the arborescents. The complete independence of the plumule with regard to the primary root stele is even better shown in the Commelinaceae. Provision for the adventitious root system to replace the radicle is made in the embryo. The complete abortion of the root in some Bromeliaceae, and its retarded development in the hydrophytes, is to be taken as directly correlated with the habit of the adult.

V. Towards economy in the vascular system of the cotyledon.

SARGANT regarded the seedlings of Liliaceae as exemplifying a central type. The double bundle derived from the fusion of strands of two cotyledons was the basis for other types. Thus "the external characters of all the Palm seedlings examined are much modified from the ordinary monocotyledonous type, by the arborescent habit of the family", and, regarding *Arum maculatum* "the vascular system of the cotyledon has been profoundly modified by its peculiar habit". Again, of Aroideae, "the succession suggested by the structure of their seedlings is from *Anemarrhena* through forms .. resembling *Chlorogalum* and *Arthropodium*/

Arthropodium to others like Allium and Zygadenus, thence to Anthurium". The interpretation, however, of the single cotyledonary strand as a reduction product of the double bundle was neglected.

Instead of regarding the double bundle as the starting point of variations in vascular anatomy, one might view it more consistently and with as much foundation as merely a stage in a lengthy reduction series.

- i. Three groups have many strands in the cotyledon, namely the Arborescents, the Aroids and large-seeded Amaryllidaceae.

It is generally admitted that the first group represents primitive types. Apart from the classification of Palms and Aroids by systematists, indications that the Aroids are a relatively primitive family are not lacking (87, 88).

As for Clivia, Crinum and members of the Amaryllidaceae resembling them in seedling anatomy, they belong to BEWS'S forest margin types, and, in his opinion, ancient and not secondary. Aberrant genera, the woody climbers, and Canna have retained primitive characteristics in the cotyledon.

- ii. Certain small-seeded Amaryllidaceae, and some Liliaceae (*Erythronium*, *Trillium*, *Paris* etc.) have three or four strands in the cotyledon. The subsidiary strands in the cotyledon sheath of certain bulbous forms, produced as its girth increases, are, however, obviously secondary in their origin.
- iii. With the exception of the Commelinaceae and Zingiberaceae, families exhibiting two strands or a double bundle in the cotyledon are confined to the Liliiflorae.

Possibly guided by chance, probably as a result of the ease with which Liliaceous seedlings are obtainable, SARGANT chose this family to provide evidence for the origin of monocotly. In attempting to visualise the same symmetry in the cotyledon of Palms and Aroids, she laid the theory open to criticism.

Plants of such widely differing habit are comprised in the Liliaceae that only the common floral construction accounts for their systematic grouping. The family is composed of genera in which the flower has reached the same stage in evolution. The postulate/

postulate of a common origin for such is unnecessary. It is equally reasonable to suppose, also, that the majority of Liliaceous seedlings are at the same evolutionary level regarding the number of vascular strands, although the reduction in the photosynthetic activities of the cotyledon has not proceeded to the same extent in all.

The argument is strengthened by the occurrence of a single strand in the Iridaceae, a family floristically advanced.

The fact that the Zingiberaceae and Commelinaceae have two strands in the cotyledon does not necessarily indicate relationship with the Liliaceae or with each other.

In the Zingiberaceae the floral characters are a marked advance on those of Liliaceae. The seedling morphology is equally progressive in that the whole family consistently possess the ligulate cotyledon. While certain genera seem to be on a level with Liliaceae in having two strands in the ligule, others show the evolutionary tendency to reduce the cotyledonary tract by shortening the course of one or both strands.

In/

In the extreme case the cotyledon is devoid of vascular tissue, save for the strands entering the suctorial tip.

iv. Seedlings with one strand in the cotyledon are the penultimate stage in this reduction series. They include -

- (a) Hydrophytes where the reduction is presumably correlated with the environment since other organs are thus affected.
- (b) Epiphytes and plants which occupy habitats presenting problems kindred to those of an epiphytic mode of life, e.g. Vellozia.

Reduction along other lines has not taken place in all the epiphytes. With the lack of a suitable substratum, hypogeal germination would be almost impossible. The ligulate type of cotyledon is not found in the aquatics. Bearing in mind the danger of implying purpose to account for plant form, one might still suggest that abbreviation of the vascular system in the circumstances would be unnecessary.

- (c) Certain genera in the Iridaceae. This group is not subjected to extremes of environment as the above associations are. The trend then may be viewed as in some measure acting distinct from the factor of habitat.

The above theory of the relationship between seedlings having different cotyledonary anatomy does not preclude SARGANT'S views on the origin of Monocotyledons. It does/

does, however, argue against her assumption that cotyledons with more than two strands were derived from the central double bundle type, and against their origin from dicotylous stock, unless it is admitted that the fusion of Dicotyledonous seed leaves took place many times, giving rise to different types of cotyledon anatomy.

The similarity of the skeletal system of *Anemarrhena* and the ranalean *Eranthis*, particularly in the transition, was regarded by SARGANT as evidence of their common origin. But angiospermous seedlings are all confronted with the same problem, namely the arrangement of strands between root and shoot in the manner consistent with available space, number of strands, phyllotaxy and number of the leaves. That certain members of both phyla have solved the problem in an identical manner does not imply the derivation of one from the other. An analogous case is the dicotyledonous arrangement of strands in the hypocotyl and stem of the young monocotyledon, from which occurrence has been deduced the dicotylous ancestry/


ancestry of the latter. Too much importance may be attached to this and the transition anatomy as signifying phylogenetic relationships.

VI. Towards direct vascular communication between cotyledon tip and plumular bud.

Billbergia (Bromeliaceae) and two genera of Zingiberaceae (*Alpinia* and *Hedychium*) afford instances in which the cotyledon may give up its entire vascular supply in order to establish this connection.

VII. Towards increasing embryonic development before germination.

This tendency is parallel to the gradual acquisition of a ligulate cotyledon, and affects not only the differentiation of the organs, but their relative orientation. In epigeal germination the cotyledon, plumule and radicle of the seedling finally lie in the same vertical straight line; the same is true in hypogeal germination, but the cotyledon tip and stalk are not in alignment with the other organs. Where the cotyledon is ligulate, however, the vertical line in which plumule and radicle lie is at right angles to the cotyledon stalk and sucker. This orientation reacts/


reacts upon the intra-seminal condition. Not only are the plumule and radicle out of alignment with the remainder of the embryo, but they lie at an obtuse angle to each other (p. ). The form of the post-seminal plant is foreshadowed in the seed.

The culmination of all these tendencies is to be found in the Grass Embryo and Seedling.

IV. THE SEEDLING OF GRAMINEAE AS THE CULMINATION OF A REDUCTION SERIES.

(1) Orientation of Organs in the Embryo.

The final orientation of the organs of a seedling of the form of *Hedychium* takes place within three days. If such a plant, instead of being free, were still enclosed by the testa and partially surrounded by endosperm, an embryo almost identical to that of the Grass would result. A stage in seedling development which normally occurs post-seminally is attained before germination has begun. The biological tendency towards protection of the embryo until it is fully equipped for an independent existence finds its fullest expression in the Gramineae. This observation on the orientation within the embryo was also made by/

by GATIN, whose work on seedling anatomy has been almost entirely ignored by later investigators. GATIN, however, apparently did not realise its significance nor the fact that the grass embryo repeats in its ontogenetic sequence the stage comparable to the day-old *Hedychium* (Fig. ).

- (2) The advanced development of plumule and adventitious root system in conjunction with marked endogeny and poor differentiation of the radicle are in accordance with the evolutionary trends discussed.
- (3) Reduction has affected the cotyledon, which consists of -
 - i. a suctorial portion, the "scutellum",
 - ii. a fragment of the sheathing base, hitherto termed the epiblast.

The cotyledon is entirely non-vascular except for the scutellum traces. Its strands have become part of the vascular system of the first internode of the plumular axis, the so-called mesocotyl.

The cotyledon possesses no ligule: the "coleoptile" is therefore the first plumular leaf. The basis for this view is revealed by a comparison of certain grass seedlings described by SARGANT and ARBER with seedlings of *Billbergia zebrina* and two genera of Zingiberaceae.

A. ALPINIA CALCARATA

1. Two strands leave the tip, proceed through stalk and at the base of plumular axis each ramifies, giving three traces.
2. The axis has a central core consisting of plumular traces plus one-third of each cotyledon strand. The latter supply the second leaf. An outer ring of four strands derived from the cotyledon supplies the first leaf.
3. The first leaf derives its total vascular supply from the cotyledon strands.

SORGHUM VULGARE

1. A single strand proceeds from the "scutellum" straight to the base of the "mesocotyl".
2. The stele of the "Mesocotyl" consists of two "coleoptile" traces (distinctly double) plus plumular traces. Part of the scutellum trace forms half of each coleoptile trace at the top of mesocotyl. The remainder is prolonged downwards towards the root.
3. The coleoptile (i.e. first leaf) derives its total vascular tissue from the cotyledon.

B. BILLBERGIA ZEBRINA

1. A single cotyledon strand proceeds from the tip, through the stalk.
2. It ascends the first internode in an independent peripheral position.
3. Towards the top it merges into the meristem of the first leaf, contributing to the lateral strands.

AVENA SATIVA

1. There is a single scutellum trace.
2. It ascends the mesocotyl as an independent peripheral strand.
3. At the top of the mesocotyl it forms part of the complex from which the two "coleoptile" strands, laterals of the "first" leaf and mid-rib of the "second" leaf arise.

4. Longitudinal sections reveal the presence of a bridge comparable to that in *Avena*.

4. The top of the scutellum trace is connected to the central stele by a xylem "bridge" or "arch".

C. HEDYCHIUM GARDNERIANUM

1. Two strands in cotyledon tip.
2. One strand proceeds horizontally to base of plumular axis where it divides -
 - i. half maintains independent peripheral position to top of the internode where it merges into meristem of laterals of first leaf and mid-rib of second leaf;
 - ii. half enters the central stele of the axis.
3. The first leaf laterals and possibly the mid-rib of the second leaf are derived from half of the cotyledonary tissue.

Represents a compromise between *Avena* and *Sorghum* in the occurrence -

- (a) of an independent peripheral scutellum trace,
- (b) of a portion of the scutellum trace becoming part of the central axis of the first internode.

CONCLUSIONS DRAWN FROM ABOVE COMPARISON.

1. The occurrence of cotyledon traces, independent or otherwise, in the first internode of the plumular axis is not unique. The need for a hypothetical mesocotyl/

mesocotyl in the Grasses does not therefore exist.

2. Leaf-like organs drawing their vascular supply, wholly or partly from the cotyledon are not necessarily cotyledonary in nature. The plumular origin of the first foliar member of *Billbergia*, exactly homologous with the "coleoptile", is indisputable.
3. The Grass seedling has no "ligule". Its cotyledon was formerly identical with that of *Hedychium*, consisting chiefly of ligule, with the stalk inserted so low that almost no sheathing base was present.

DERIVATION OF THE GRASS COTYLEDON
FROM THAT OF THE HEDYCHIUM TYPE.

1. Tangential pressure on the club-shaped sucker of *Hedychium* will produce the fleshy plate (scutellum) of the Grass.
2. As a result of the same acting force the short stalk (almost non-existent) in *Hedychium*, will completely disappear.
3. If, in *Hedychium*, that side of the ligule remote from the sucker becomes thinner, until finally in the/

the weakest region the tissue ceases to develop, only a fragment (the epiblast) will persist on one side. The other side of the ligule will be contiguous with the sucker, with which it will, therefore, fuse. The plasticity of the latter will be advantageous for this union.

Evidence for such a derivation of the Grass cotyledon is found in that organ itself.

- i. The Epiblast may be non-existent (*Zea*), a thin scale barely discernible, or a leaf-like organ clasping round the "mesocotyl" half way, with its tip on the level of the base of the coleoptile (*Zizania aquatica*). In extreme cases (*Leersia clandestina*) the epiblast may extend almost to the top of the coleoptile. Reduction has, therefore, progressed to varying degrees in the different genera. VAN TIEGHEM'S research indicates that two-thirds of the grasses have an epiblast, while BRUNS'S tables on the frequency with which it occurs reveal an interesting sequence with the exception of *Oryzeae*. Tribes of HACKEL'S first series have, as a rule, embryos with no epiblast. It is found with very few exceptions in the remaining tribes. These comprise HACKEL'S second series, which, according to BEWS, contains most primitive/

primitive forms. *Hordeum* and *Triticum* at the end of the second series have two strands in the cotyledon and an epiblast. *Zea Mays* at the beginning of the first series has no epiblast, and only one vascular strand: it thus appears as the final stage in the gradual loss of the ligule and reduction of vascular tissue.

- ii. In certain instances the orientation of the ripe embryo is only slightly in advance of that of the *Hedychium* type. Epiblast and scutellum are then of equal length, (giving an appearance which misled COULTER to a discovery of "dicotyledony"). A bridging of the short gap between them would complete the ligule (Fig. ~~x~~). Stages comparable to this occur in the early ontogeny of the advanced types. Further differentiation and growth of the embryo result in a widening of the distance between the two parts of the cotyledon.
- iii. The remainder of the non-vascular ligule, in fusing with the flat sucker, lost its identity almost completely. An indication of its former separate existence is given by the short overhanging protuberance at the upper limit of the scutellum, sometimes designated "the ventral scale". PERCIVAL, regarding the scutellum as
a/

a foliage leaf, terms it "the ligular scale". Like the epiblast, its development is variable. It is very marked in *Bambusa*, floristically the most primitive genus, of which the embryo is ontogenetically backward. In embryos with large epiblasts it is prominent and does not appear where the former is missing. In a very significant figure of an immature embryo of *Oryza sativa* by BRUNS, a deep cleft occurs between the outer layer of the scutellum and the lengthy protuberance (Fig. ~~X~~). It is thus evident that the ventral scale represents the apex and often in addition part of the aborted portion of the former ligule, now limited to the epiblast and to the inner layer of the scutellum. The outer layer of the latter was the sucker; it includes the vascular tissue and is bounded by the epithelium. The sucker in its original form may not have been club-shaped as in *Hedychium*. *Musa* furnishes an example of a sucker shaped like a plate.

- iv. The forking of the coleoptile in certain grasses is not, in itself, an argument for its being the first leaf, but gives support to it.

V. PROBABLE FACTORS IN DETERMINING
THE CONFIGURATION OF THE COTYLEDON
OF THE GRASSES

1. A balance is maintained between the embryonic organs. Inordinate development of the plumule affects the radicle. It may in addition react adversely on the cotyledon.
2. The mature embryo represents a phase which in other Monocotyledons takes place post-seminally. Unlimited expansion would normally be available. The firm pericarp and mass of endosperm place restrictions upon it: these were probably the most potent factors in altering the shape of the cotyledon. Distortion from the normal Hedychium type is least in the very early stages.
3. The position of the embryo in the seed accounts for its shape. Subjected to pressure from the endosperm side, the organs most affected will be -
 - i. the sucker and the half of the ligule on that side,
 - ii. the portion of the ligule forced against the wall. The lack of endosperm in this neighbourhood, and the downward extension of the epiblast in certain embryos are thereby explained.

The apex of the radicle and of the ligule will be least affected. The vestigial remains of the latter/

latter have therefore persisted.

The coleorhiza does not merit a discussion, its existence is clearly the result of the endogeny of the radicle.

VI. POSSIBLE CRITICISMS OF THE FOREGOING ARGUMENT.

- i. That the venation of the coleoptile is inconsistent with that of an independent plumular leaf.

(Used by WORSDELL of COULTER'S Theory).

The first scale leaf of Romulea and the coleoptile are identical in venation.

- ii. That there exists a greater difference between the coleoptile and the first leaf than between the latter and succeeding leaves. (WORSDELL criticising COULTER).

A survey of the first leaves described in this thesis refutes this argument. Second and third plumular leaves may, in addition to the first, be of the nature of scale leaves (p. 226).

- iii. That HEGELMAIER and HANSTEIN observed that "the rudiments of the coleoptile arise in the tissue complex which is becoming the scutellum".

(WORSDELL)

In a similar manner the first leaf of any monocotylous embryo would appear to arise from the surrounding cotyledon/

cotyledon tissue. The distortion in the plumular region of the embryo, and frequently the lack of cotyledonary tissue to sheathe the bud, has obscured the true origin and nature of the "coleoptile".

- iv. That no instance can be given in which the epiblast and ventral scale actually fuse.

A line of future research is suggested by this. The search for an embryo showing such a fusion may be fruitless since the gap in the ligule possibly corresponds to a slit such as occurs in numerous cotyledons for the emergence of the first leaf.

VII. THE POSITION OF THE PRESENT THEORY IN RELATION TO PREVIOUS INTERPRETATIONS OF THE GRASS EMBRYO.

1. In its conception of the nature of mesocotyl and coleoptile it is akin to that of BRUNS and COULTER, but the latter accepted the plumular nature of these organs as a corollary to their belief that the epiblast was a second cotyledon and not on anatomical grounds.
2. It accounts in a consistent manner for the epiblast and ventral scale where these occur, and for their absence in the advanced types. That the epiblast is/
is/

is a scutellar outgrowth (*2*) or foliar organ such as occurs at the base of the axis of *Sedum* (CELAKOVSKY) is incompatible with its position which would inhibit the production of new structures.

3. The difficulties which had to be explained away by SARGANT and ARBUR on their assumptions, no longer arise, e.g. the anatomical difference between the "mesocotyl" of *Sorghum* and *Avena*, the absence of mesocotyl in *Hordeum* and *Triticum*, the "xylem arch" at the top of the mesocotyl in *Avena*. The bud axillary to the coleoptile which HOWARTH found in *Festuca rubra* no longer calls for comment: it is merely in the axil of a plumular leaf.
4. The necessity for the phylogenetic relationship between Zingiberaceae and Gramineae, suggested by SARGANT and ARBUR, to explain similarity in seedling structure does not exist since the grass type occurs in Bromeliaceae as well as in Zingiberaceae. A more striking example of parallel development is difficult to find.
5. The grass embryo regarded from the new standpoint is in closer conformity with the general Monocotyledonous type than before.

C O N C L U S I O N

1. The main trend of the Monocotyledonous seedling is towards precocious development of the plumule, abortion of the radicle and consequent importance of an early adventitious root system.
2. The vascular tissue of the cotyledon is disappearing, a phenomenon illustrative of convergent evolution since it occurs in unrelated families. It may be regarded:-
 - i. as a progressive tendency, because the plumule is thereby benefited;
 - ii. as an indication that the Monocotyledons are a phylum of decadents, or the residuum of a stock now incapable of change save in the direction of reduction or curtailment. The wealth of structural detail revealed in the seedling is an added argument for this point of view.
3. The habit of the adult may act as a differentiating factor in three ways -
 - i. as an aid to the reduction process. The equipment of the embryo and young seedling for a geophytic existence in the manner described is doubtless connected with increasing xeromorphy/

xeromorphy of the adult.

- ii. as a check on the reduction process, in order that organs necessary for the mode of life of the adult be retained, e.g. a lengthy tap root in young bulbous plants.
 - iii. as a direct and forceful cause of reduction in individuals, e.g. aquatics and epiphytes, quite apart from its more ancient and widespread effect in directing in an almost imperceptible fashion the evolutionary trend.
4. To the voluminous literature on the origin of Monocotyledons there is little to add. The single cotyledon is undergoing reduction; it may be argued, therefore, that it arose primarily from the reduction or fusion of two cotyledons. If so, the assumption that such a union produced a central type does not account for the anatomy of primitive seedlings. The sequence revealed by this research points to the derivation of the phylum from an ancestor having numerous cotyledonary strands, or to the alternative of their polyphyletic origin.

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The above list refers to works consulted.
A more complete account of papers relating
to this subject is given by SARGANT and
ARBUR (102), and WORSDELL (130).

NOTE: The six references marked (*) have not been
read in the original.
